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Morphology and biometry of twelve soil testate amoebae (Protozoa, Rhizopoda) from Australia, Africa, and Austria

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Synopsis. The morphology of 12 species of testate amoebae from soils of Australia (*Bullinularia gracilis, Centropyxis cryptostoma, Heleopera sylvatica, Assulina muscorum, Corythion asperulum, Euglypha compressa*), Africa (*Paraquadrula irregularis*) and Austria (*Cyclopyxis kahli, Difflugia stoutii, Nebela tubulata, Tracheleuglypha dentata, Trinema enchelys*) were investigated by light and scanning electron microscopy. All species are characterized morphometrically and an 'ideal individual' for each species is constructed by means of the morphometric data. A first record for Austria is *Difflugia stoutii*, first records for Australia are *Bullinularia gracilis, Centropyxis cryptostoma, Corythion asperulum* and *Heleopera sylvatica*. In *P. irregularis*, numerous cells united at their apertures have been observed. Protargol silvered material convincingly shows fusion of the nuclei and nucleoli of such pairs. It is, however, uncertain whether the uniting cells are parent and daughter (autogamy) or are from 2 different specimens (conjugation).

INTRODUCTION

Many species of testate amoebae have been described and redescribed without providing reliable biometric data. The present paper is the second (Lüftenegger et al., 1988*a*) of a series of publications intended to improve the diagnosis of such species. This hopefully will also help ecologists with the often difficult species determinations.

MATERIALS AND METHODS

For the sources of material see Table 1. Testate amoebae were isolated with a pipette as individuals from soil suspensions (0.2 g fresh soil + 5 ml distilled water) and stained either with protargol silver or phenolic aniline blue solution (Foissner, 1983; Lüftenegger et al., 1988*b*). The shells of some species were made transparent overnight in a drop of albumin-glycerin (as used in histological techniques to fix sections on a slide). All drawings were produced with the help of a camera lucida using an oil immersion objective (100 ×; eyepiece, 10 ×) and bright field illumination.

The following sample statistics were calculated according to Schönborn et al. (1983): $\bar{x}$, arithmetic mean; M, median (this value is used to construct the ideal individual); SD, standard deviation; SE, standard error of the arithmetic mean; CV, coefficient of variation in %; Min, Max, minimum and maximum values; n, sample size. Most shell variables were given a number which defines the corresponding character in the drawing of the ideal individual. The respective characters are identified by these numbers in the tables (Lüftenegger et al., 1988*a*).

For scanning electron microscopy specimens were cleaned by several transfers through distilled water before being manipulated by a single-hair brush as individuals and mounted on glass slides covered with a special adhesive (Mixtion à Dorer Clarifeé, Fa. Lefranc & Bourgeois). Further procedures see Lüftenegger et al. (1988*a*).

Determinations of species follow the original descriptions. One slide of each population has been deposited in the British Museum (Natural History) in London. Registration number is given in the species description. Several species have the same Reg. No since they are on the same slide.

Table 1. Localities of the populations.

Species Reference number	Date	Locality
Bullinularia gracilis	23.10.1986	Bush in the Brisbane Water National Park, 50 km north of Sydney, Australia. E 152° S 33°. Sea-level 150 m. Upper soil layer (0–2 cm soil depth) with litter and moss on sandstone. pH 5.1.
Centropyxis cryptostoma	23.10.1986	See *Bullinularia gracilis*.
Cyclopyxis kahli	10.10.1987	Aiglern near Aigen in the Ennstal, Austria, E 14° N 48°. Sea-level 650 m. Brown earth (loamy sand) of a meadow (0–5 cm). pH 6.7. (For detailed site description see Foissner et al., 1990).
Difflugia stoutii	10.10.1987	See *Cyclopyxis kahli*.
Heleopera sylvatica	18.10.1986	Coastal wood, Royal National Park, south of Sydney, Australia, E 150° S 35°. Sea-level *c.* 100m. Upper soil layer (0–5 cm) with litter and brown sand. pH 4.5.
Nebela tubulata	20.9.1988	Top of the Gaisberg, Salzburg, Austria, E 13° N 48°. Sea-level 1250 m. Rendzina of a spruce forest with *Luzula*, *Calamagrostis*, *Sesleria* (0–5 cm). pH 5.2.
Paraquadrula irregularis	8.5.1985	Mzima Springs, Tsavo National Park West, about 50 km east of Mt. Kilimanjaro, Kenya, E 38° S 4°. Humus layer with litter, many fungi, under acacia (0–5 cm). pH 7.0.
Assulina muscorum	23.10.1986	See *Bullinularia gracilis*.
Corythion asperulum	23.10.1986	See *Bullinularia gracilis*.
Euglypha compressa	23.10.1986	See *Bullinularia gracilis*
Tracheleuglypha dentata	10.10.1987	See *Cyclopyxis kahli*.
Trinema enchelys	10.10.1987	See *Cyclopyxis kahli*.

DESCRIPTION OF SPECIES

Bullinularia gracilis Thomas, 1959

Figs 1–8, Tables 1,2

BM (NH) Reg. No. 1990. 4. 26.1.

Shell yellowish to brownish, almost hemispheric, always broader than long, ventral side smooth, structureless, covered by thin, fragile layer (Fig 7), posterior margin and dorsal side rough, covered with xenosomes (Figs 4,5). Aperture obscured by anterior lip, under which ventral side projects (Fig. 6). Approximately 30 pores, about 1–2 μm in diameter, irregularily arranged in the anterior third of shell (Fig. 8).

Characters (1)–(3) show normal variability (CV 14.0 and 12.3%), whereas characters (4) and (5) have high coefficients of variation (CV 20.0 and 30.0 %; Table 2). Thomas (1959) states 120 μm on average for the major axis of the shell. The specimen photographed by Bonnet (1961) shows a similar size, however, detailed biometric data are not provided. Regarding this character, the values of our population are about 25 % higher, which is in agreement with Golemansky (1968).

Table 2. Morphometric characterization of *Bullinularia gracilis*. All measurements in μm.

Character	$\bar{x}$	M	SD	SE	CV	Min	Max	n
(1)	93.2	88.5	13.0	5.33	14.0	83	118	6
(2)	130.3	125.0	18.2	4.70	14.0	112	169	15
(3)	150.9	150.0	18.5	4.78	12.3	128	192	15
(4)	57.1	54.0	11.4	2.94	20.0	41	80	15
(5)	11.5	10.0	3.4	0.89	30.0	5	16	15

Hoogenraad & De Groot (1952*b*) describe two shell types for *B. indica*. The 'extraordinary' type is firm and inflexible, the 'normal' type is flexible and rather tenacious, consisting of a homogenous matrix, as stated also by Penard (1912). We suggest that the outer organic layer, which seems to be somewhat elastic (Fig. 7), is responsible for the above mentioned flexibility of shells in some *Bullinularia* populations.

Centroypyxis cryptostoma Bonnet, 1959

Figs 9–13, Tables 1,3

BM (NH) Reg. No. 1990. 4. 26.2.

Shell brownish, rectangular with rounded ends in ventral view, compressed, ventral side fairly smooth, with flat xenosomes, dorsal side with rough particles. Aperture sub-apical, reniform. Posterior lip extends slightly inside shell as curved elongation of ventral side, anterior lip overhanging (Figs 10,12). Separation from *C. capucina* and *C. halophila* is mainly by smaller size and occurrence in different habitats (pH optimum for *C. halophila* 8.5–9; Bonnet & Thomas, 1960*a*).

Coefficients of variation of characters (1)–(4) and (7) are less than 10 %; measurements of aperture show greater variability (CV 12.5 and 14.9; Table 3). Bonnet (1959) states 45 μm for the length, 35 μm for the breadth and 27–30 μm for the depth of the shell. The individuals of our population are a little more flattened, which is in agreement with the measurements by Schönborn (1966). All other characters match well with the description by Bonnet (1959).

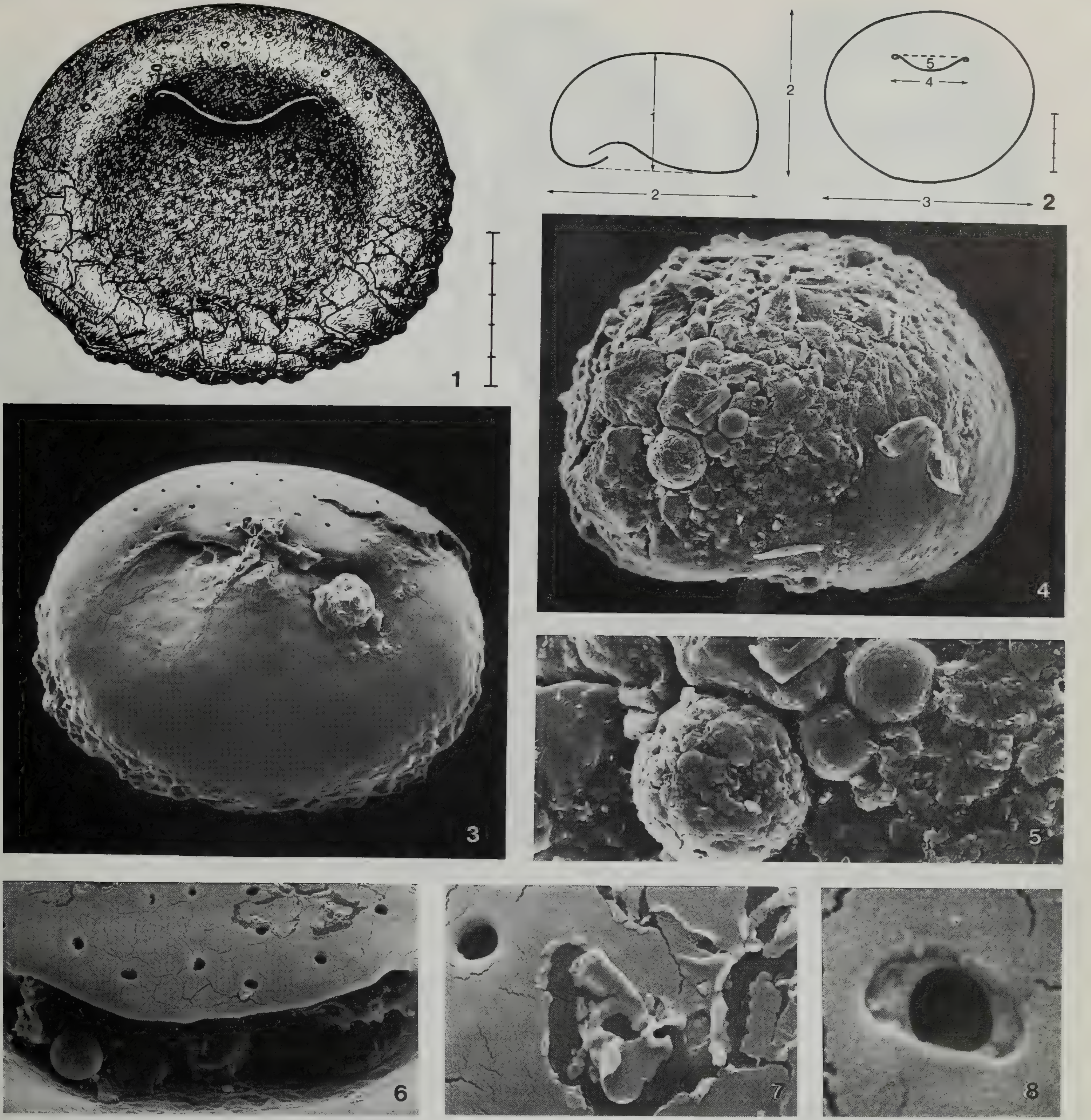
Cyclopyxis kahli (Deflandre, 1929) Deflandre, 1929

Figs 14–16, Tables 1,4

BM (NH) Reg. No. 1990. 4.26.3

Shell brownish, hemispheric, composed of xenosomes, apertural surface smooth and distinctly invaginated, aboral surface rough. Aperture surrounded by distinct rough particles (10–20 % of specimens studied), or more or less smooth (c. 80–90 %).

Shell measurements fairly variable (CV 10.6–16.0; Table 4). The data of Deflandre (1929) and Ogden (1988) agree well with ours, whereas other authors state slightly higher values (Bonnet & Thomas, 1960*a*; Ogden & Hedley, 1980; Ogden, 1984; Rauenbusch, 1987). The Indian population described by Guru & Dash (1983) measures only 50–65 μm in diameter (sample size not given).



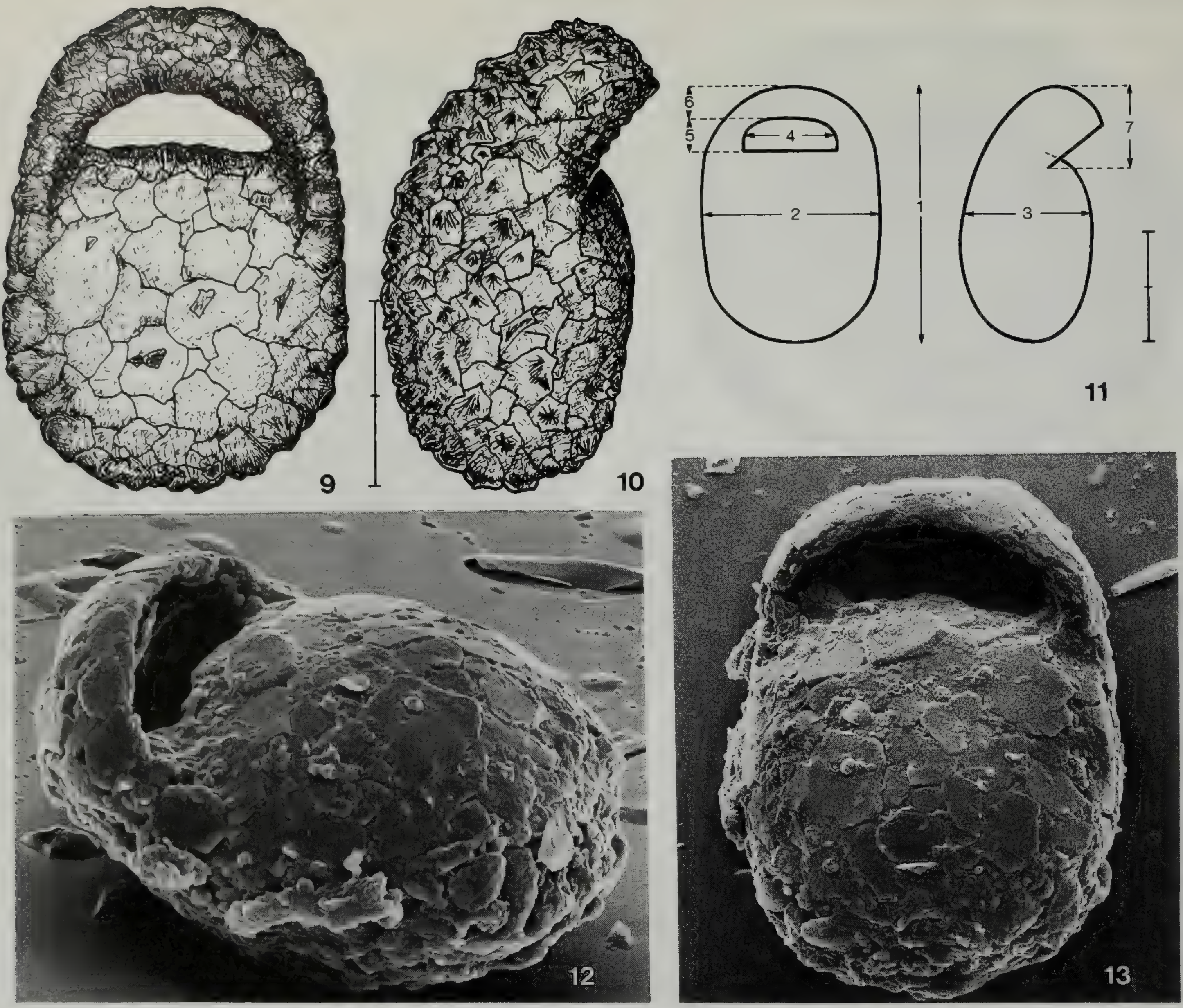
Figs 1–8 ***Bullinularia gracilis***, light microscopic (Fig. 1) and SEM-aspects (Figs 3–8) and ideal individual (Fig. 2). **1** Ventral view. **2** Lateral and ventral view. **3** Ventral view, × 400. **4** Lateral view, × 500. **5** Detail of rough dorsal shell surface, × 1500. **6** Aperture, × 1200. **7** Detail of smooth ventral shell surface, × 3700. **8** Pore, × 12000. Scale bar divisions 10 μm.

Table 3. Morphometric characterization of *Centropyxis cryptostoma*. All measurements in μm.

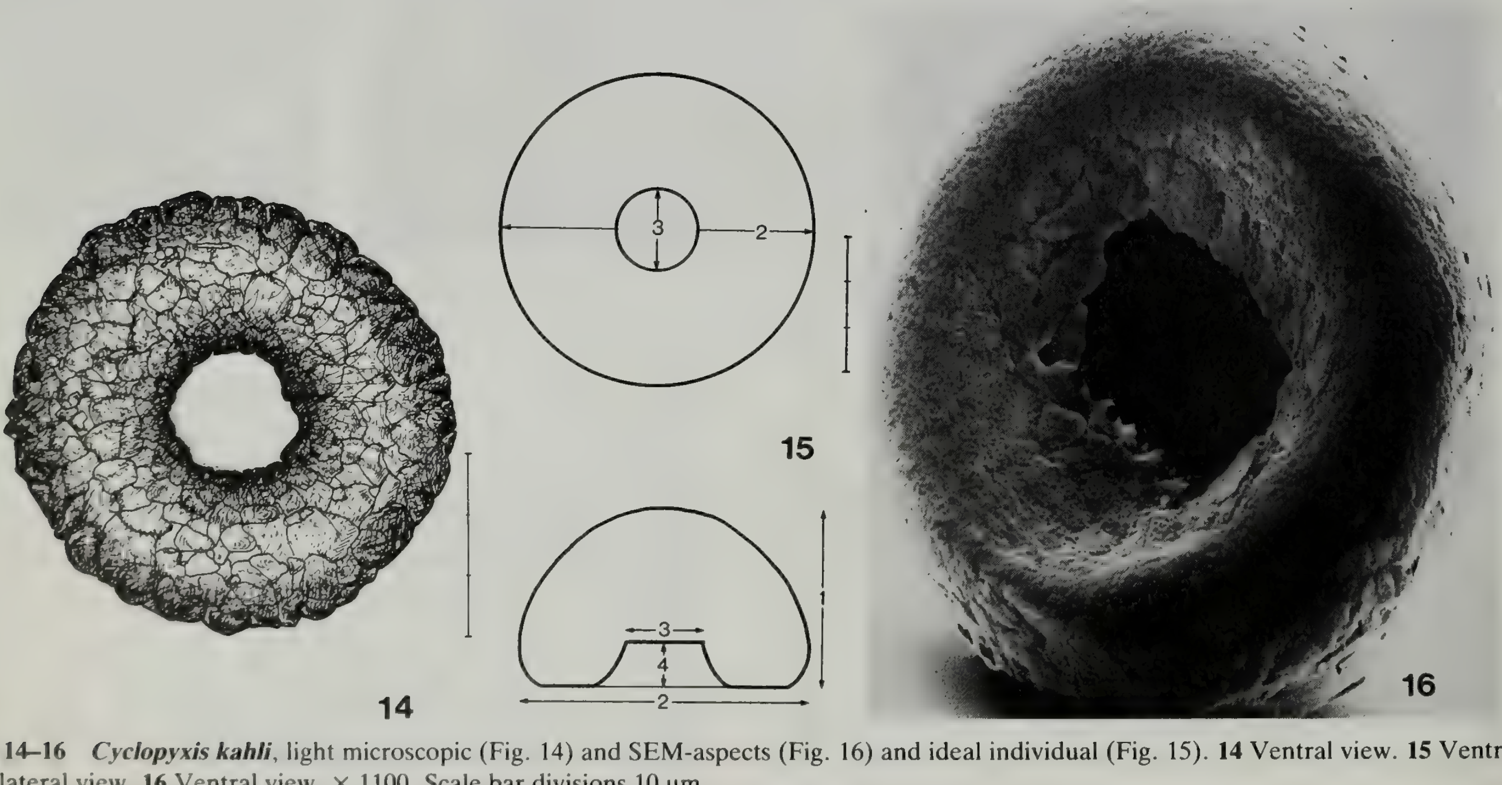
Character	x̄	M	SD	SE	CV	Min	Max	n
(1)	46.1	46.0	2.0	0.64	4.4	42	48	10
(2)	32.4	32.0	2.6	0.82	8.0	28	35	10
(3)	23.2	22.5	2.0	0.65	8.8	20	27	10
(4)	15.4	16.0	1.4	0.45	9.3	13	18	10
(5)	6.4	6.3	0.9	0.30	14.9	5	8	10
(6)	5.6	6.0	0.7	0.22	12.5	4	6	10
(7)	14.7	15.0	1.4	0.45	9.7	13	17	10

Table 4. Morphometric characterization of *Cyclopyxis kahli*. All measurements in μm.

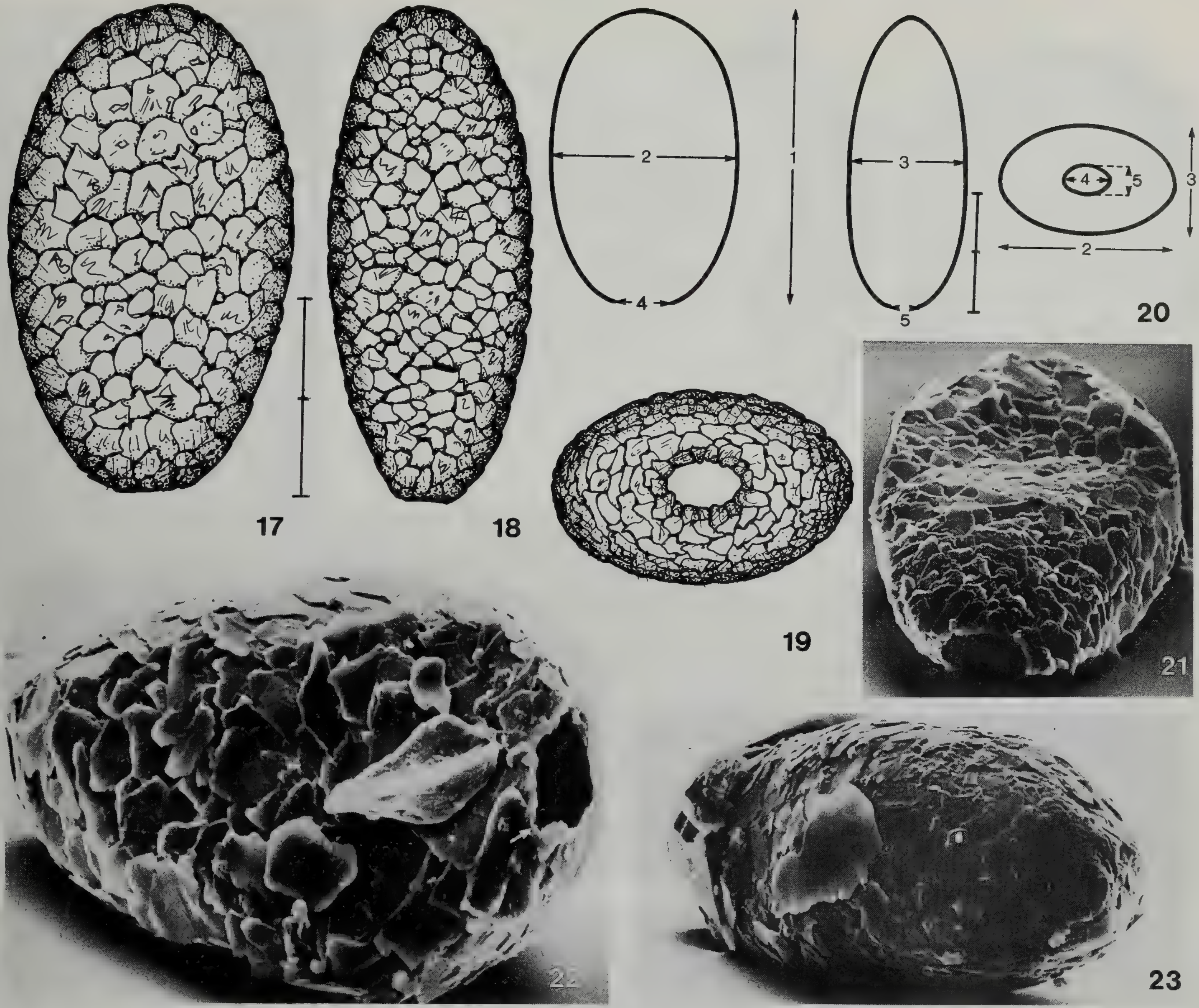
Character	x̄	M	SD	SE	CV	Min	Max	n
(1)	44.3	45.0	5.6	1.16	12.6	35	54	23
(2)	70.1	70.0	7.5	1.41	10.6	58	89	28
(3)	18.0	19.0	2.5	0.51	13.8	13	22	24
(4)	11.8	11.5	1.9	0.47	16.0	10	16	16



Figs 9–13 ***Centropyxis cryptostoma***, light microscopic (Figs 9,10) and SEM-aspects (Figs 12,13) and ideal individual (Fig. 11). **9–11** Ventral and lateral views. **12,13** Ventro-lateral and ventral view, × 1900, × 1600. Scale bar divisions 10 µm.



Figs 14–16 ***Cyclopyxis kahli***, light microscopic (Fig. 14) and SEM-aspects (Fig. 16) and ideal individual (Fig. 15). **14** Ventral view. **15** Ventral and lateral view. **16** Ventral view, × 1100. Scale bar divisions 10 µm.



Figs 17–23 ***Difflugia stoutii***, light microscopic (Figs 17–19) and SEM-aspects (Figs 21–23) and ideal individual (Fig. 20). **17–20** Broad lateral, narrow lateral and ventral views. **21** Ventral view, × 1200. **22,23** Broad and narrow lateral view, × 1600, × 1200. Arrow marks aperture. Scale bar divisions 10 μm.

Table 5. Morphometric characterization of *Difflugia stoutii*. All measurements in μm.

Character	x̄	M	SD	SE	CV	Min	Max	n
(1)	50.7	50.0	7.1	1.36	14.0	38	61	27
(2)	31.0	32.0	5.3	1.07	17.0	22	40	24
(3)	20.0	20.0	3.0	0.78	15.1	16	25	15
(4)	8.6	8.5	1.6	0.39	18.9	6	10	16
(5)	5.4	5.0	0.5	0.20	9.8	5	6	7

Table 6. Morphometric characterization of *Heleopera sylvatica*. All measurements in μm.

Character	x̄	M	SD	SE	CV	Min	Max	n
(1)	65.3	65.0	3.0	0.62	4.5	59	70	23
(2)	44.0	44.0	2.2	0.46	5.0	39	48	23
(3)	28.7	29.0	2.3	0.47	7.9	25	33	23
(4)	3.4	3.0	0.9	0.19	26.9	2	5	23

Bonnet & Thomas (1960*b*) described a variety, *cyclostoma*, lacking the rim of rough particles around the aperture. We suggest that such elements are easily lost, since transitions in the formation or reduction of the apertural rim are common (see above and Coûteaux, 1976, Fig. 1J; Ogden & Hedley, 1980, Pl. 24; Rauenbusch, 1987 Pl. 16, Fig. a). At the present state of knowledge it seems wise to classify our population as *C. kahli*.

For detailed ecological data see Bonnet (1989*a*).

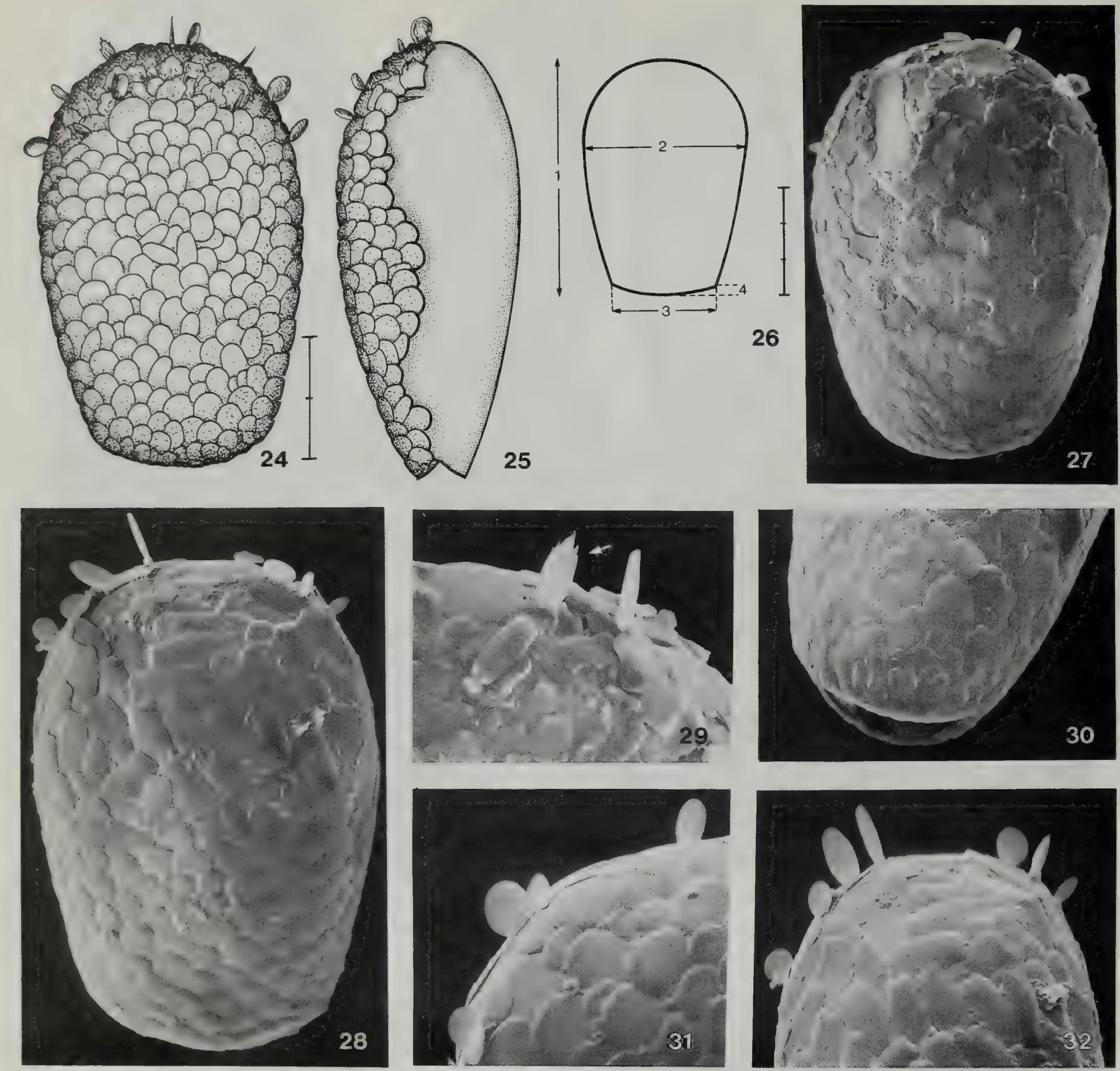
Difflugia stoutii Ogden, 1983

Figs 17–23, Tables 1,5

BM (NH) Reg. No. 1990. 4.26.4

Shell brownish, elongate ellipsoid, slightly flattened, composed of overlapping, flat xenosomes, very fragile, thus shells often collapse when air-dried (Fig. 21). Aperture elliptic.

Shell measurements, especially characters (2) and (4), show considerable variability (Table 5). Ogden (1983), who



Figs 24–32 ***Heleopera sylvatica***, light microscopic (Figs 24,25) and SEM-aspects (Figs 27–32) and ideal individual (Fig. 26). **24, 25** Broad and narrow lateral view. **26** Broad lateral view. **27,28** Broad lateral views, × 1000, × 1200. **29** Detail of surface, × 2100. Note euglyphid apertural platelet (arrow). **30** Aperture, × 1200. **31,32** Details of surfaces, × 1800, × 1200. Scale bar divisions 10 µm.

discovered this species in a *Sphagnum* sample from North Wales (England), states the following values (n = 4): 47–59 µm length, 33–36 µm breadth, 9–12 µm diameter of aperture. Our measurements agree well with those data (Table 5). However, our population is slightly compressed and has an elliptic aperture, possibly caused by living in the soil.

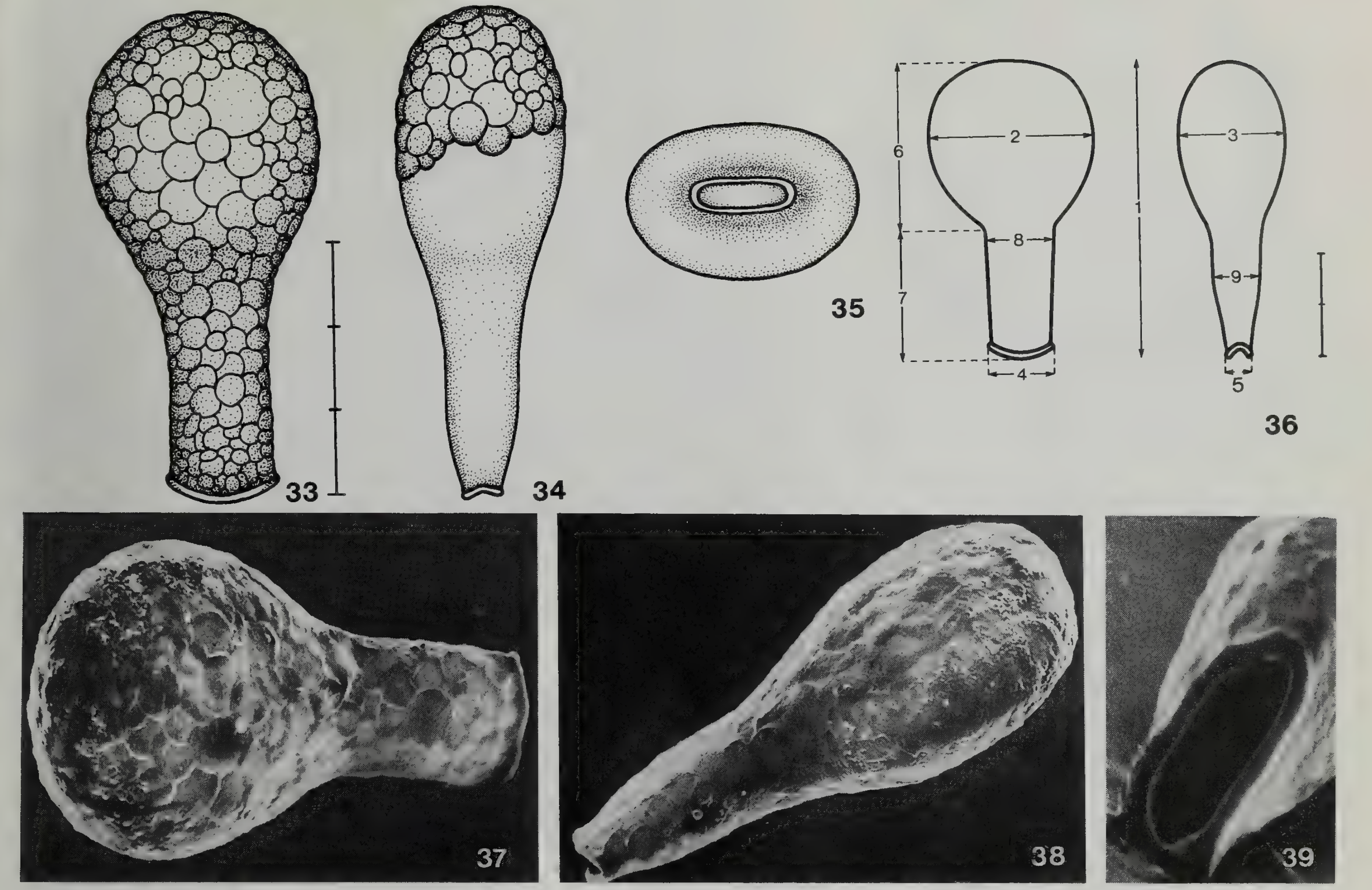
As far as we know, this is the first record since the original description.

Heleopera sylvatica Penard, 1890

Figs 24–32, Tables 1,6
BM (NH) Reg. No. 1990.4.26.5

Shell slightly yellowish, transparent, obovoid, flattened about 2:1, composed of siliceous shell platelets from other testaceans and sometimes rough xenosomes, found mainly in aboral region. Some individuals are completely covered with such acquired idiosomes (Fig. 28). The aboral region often has euglyphid platelets (*Euglypha, Trinema*) extending at right-angles like spines (Figs 28,29,31,32). Aperture terminal, slightly convex in broad view, slit-like to elliptic with small border of organic cement (Fig. 30). Nucleus with several nucleoli (protargol impregnation).

Shell measurements with exception of character (4) are fairly constant (Table 6) and agree well with the data of Penard (1890). Cash & Hopkinson (1909) state a smaller shell breadth (25–30 µm).



Figs 33–39 ***Nebela tubulata***, light microscopic (Figs 33–35) and SEM-aspects (Figs 37–39) and ideal individual (Fig. 36). **33–35** Broad lateral, narrow lateral and ventral view. **36** Broad and narrow lateral view. **37,38** Broad and narrow lateral view, × 1100, × 1200. **39** Aperture, × 2500. Scale bar divisions 10 μm.

The drawings in Penard (1890, Pl. VIII, Figs 79,80,84,86,87) clearly show individuals having peculiar spine-like structures in the aboral region and are even mentioned in his description. Hoogenraad & De Groot (1940) also state 'eigentümliche dornartige Fortsätze' for *H. petricola*, and Penard (1890) assumes very narrow idiosomes erected on the shell surface for *H. picta*. This suggestion is now confirmed by means of scanning electron microscopy. No other study describing such platelets is known to us. The paper by Coûteaux & Munsch (1978, Pl. III, Fig. 3), however, includes a scanning electron micrograph of a specimen designated as *Placocista lens*. We suggest that it is a *Heleopera* with spine-like siliceous platelets. (Unlike to *Heleopera*, the genus *Placocista* is an euglyphid taxon, having filose pseudopodia and shells with regularly arranged, self-made platelets). Presumably, all species of the genus *Heleopera* have the ability to erect platelets.

For detailed ecological data see Bonnet (1989*b*).

Nebela tubulata Brown, 1910

Figs 33–39, Tables 1,7

BM (NH) Reg. No. 1990.4.26.6

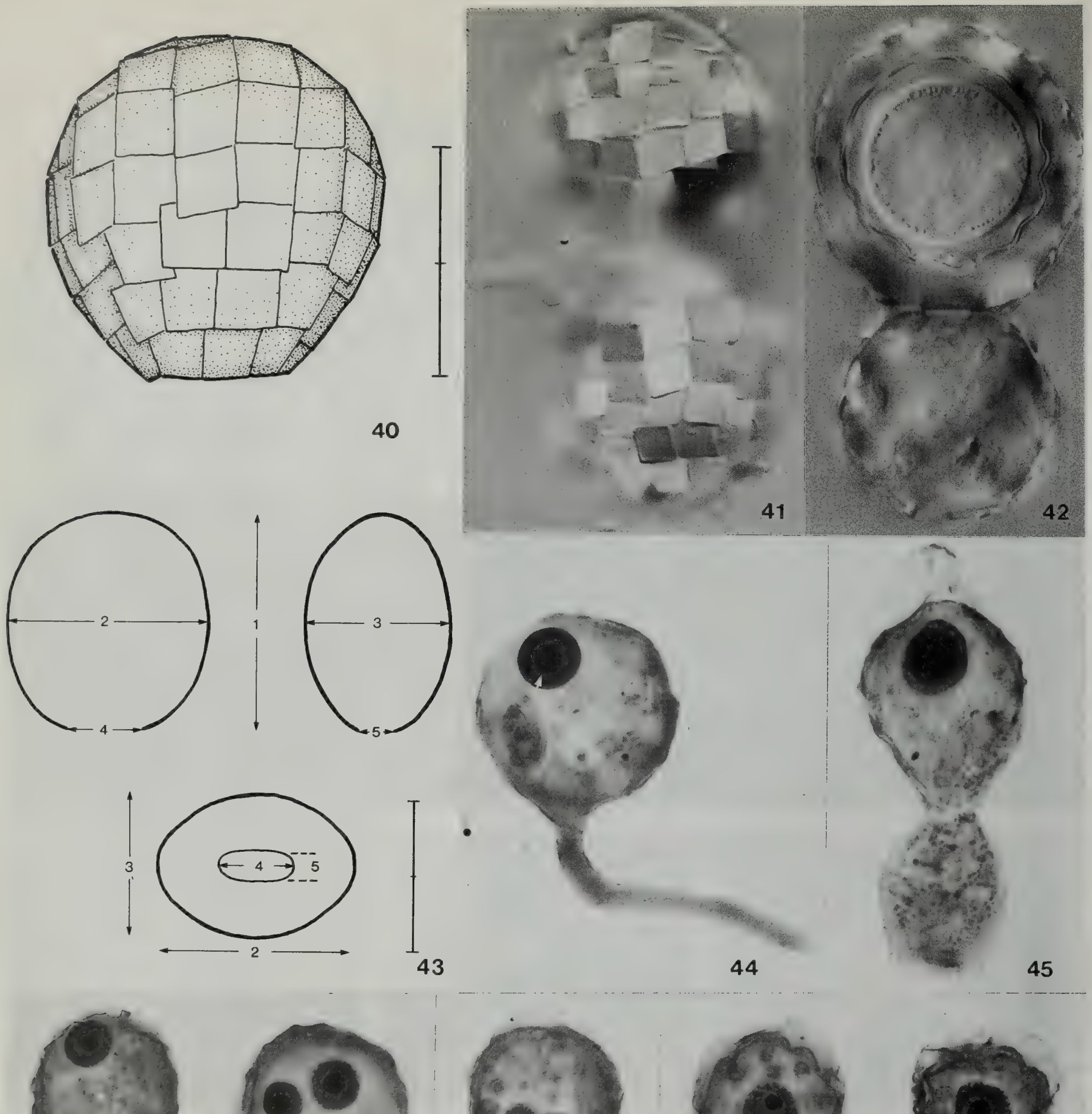
Shell colourless, flask-like with distinctly separated, parallel-sided neck, slightly compressed, fragile, composed of different sized circular and elliptic platelets from other testaceans (Fig. 33). Aperture terminal, elongate elliptic, concave in lateral view, surrounded by organic collar (Fig. 39).

Table 7. Morphometric characterization of *Nebela tubulata*. All measurements in μm.

Character	x̄	M	SD	SE	CV	Min	Max	n
(1)	60.6	61.0	2.1	0.58	3.5	57	64	13
(2)	31.4	32.0	2.5	0.69	8.0	28	38	13
(3)	22.2	22.0	2.5	1.11	11.2	20	26	5
(4)	14.3	14.0	0.9	0.24	6.2	13	16	13
(5)	5.1	5.0	0.8	0.23	15.1	4.5	6	11
(6)	33.9	34.0	2.4	0.65	7.0	29	37	13
(7)	26.5	26.0	2.0	0.55	7.5	22	29	13
(8)	14.5	14.0	1.6	0.43	10.7	12	17	13
(9)	9.6	10.0	1.5	0.57	15.8	9	12	7

Shell measurements with exception of characters (5) and (9) are fairly constant (Table 7). Character (1) has lowest variability (CV 3.5). Our values agree well with those of Brown (1910), Wailes & Penard (1911), Deflandre (1936), Hoogenraad & De Groot (1940, 1952*a*), Gauthier-Lièvre (1957) and Ogden & Hedley (1980).

Nebela tubulata is separated from *N. lageniformis* by its smaller size (*N. lageniformis* always larger than 90 μm), and from *N. militaris* by the abrupt narrowing of the shell



Figs 40–50 ***Paraquadrula irregularis***, light microscopic aspects of living (Figs 40–42) and protargol silver impregnated specimens (Figs 44–50), and ideal individual (Fig. 43). **40** Broad lateral view. **41,42** Light microscopic photographs of specimens united at their apertures, both × 1500. Note cyst in Fig. 42. **43** Broad lateral, narrow lateral and ventral view. **44** Specimen showing 1 pseudopodium. Note nucleus with central nucleolus (arrow). **45** Dividing cell. **46** Parent and daughter cell. Note microfilaments stretching between cells (arrows). **47** Fusion of 2 cells. **48** Nuclear fusion. **49** Early stage of encystation; nucleus contains 2 nucleoli. **50** Resting cyst; nucleus contains 1 nucleolus. Figs 44–50 × 1000. Scale bar divisions 10 µm.

Table 8. Morphometric characterization of *Paraquadrula irregularis*. All measurements in µm.

Character	x̄	M	SD	SE	CV	Min	Max	n
(1)	29.3	29.0	2.2	0.47	7.4	26	32	21
(2)	26.6	26.0	1.9	0.41	7.0	24	30	21
(3)	19.3	19.0	1.2	0.30	6.2	16	21	16
(4)	10.3	10.0	1.5	0.36	14.8	8	13	18
(5)	3.9	4.0	1.0	0.27	24.9	3	6	13
Platelets, length	5.9	6.0	0.9	0.19	15.1	4.5	8	21

towards the parallel-sided neck. Lateral pores as found by Hoogenraad & De Groot (1940) in some individuals did not occur in our population.

Paraquadrula irregularis (Archer, 1877) Deflandre, 1932

Figs 40–50, Tables 1,8

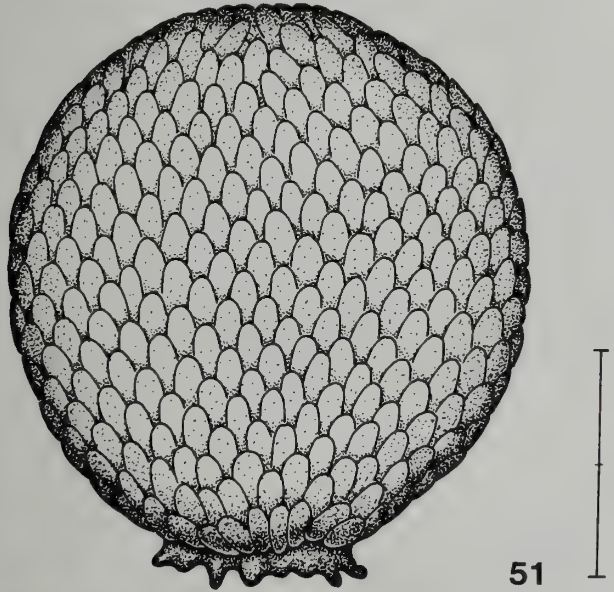
BM (NH) Reg. No. 1990.4.26.7

Table 9. Morphometric characterization of *Assulina muscorum*. All measurements in µm.

Character	x̄	M	SD	SE	CV	Min	Max	n
(1)	43.0	42.0	5.0	1.12	11.6	38	53	20
(2)	32.3	31.0	5.1	1.13	15.6	26	45	20
(3)	18.3	19.0	1.7	0.44	9.5	16	22	16
(4)	8.5	8.0	2.0	0.44	23.2	6	13	20
(5)	4.8	5.0	0.8	0.21	17.3	4	6	16
(6)	3.1	3.0	0.9	0.22	29.0	2	5	16

shell colourless, transparent, circular in broad view, slightly flattened laterally, composed of more or less quadratic calcareous platelets, sometimes irregularly arranged (Figs 40,42). Aperture elliptic. Nucleus with central nucleolus. Separation from the very similar *P. discoides* by lesser flattening in *P. irregularis*.

Characters (1)–(3) fairly constant, while measurements of



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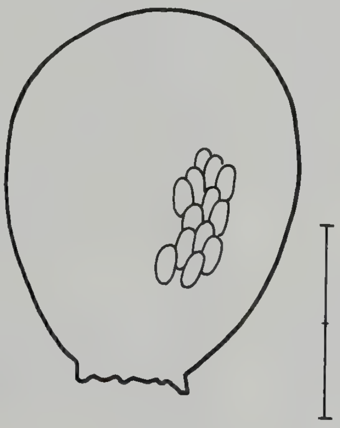

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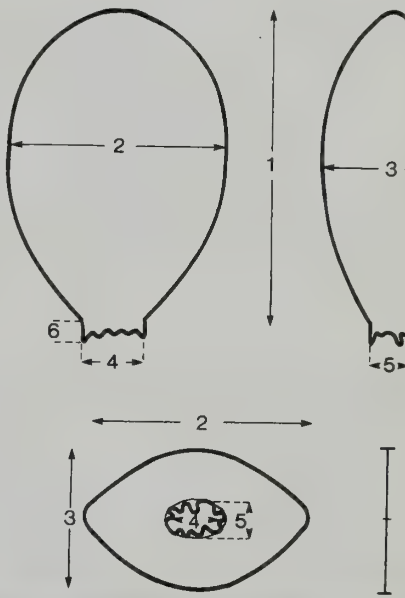

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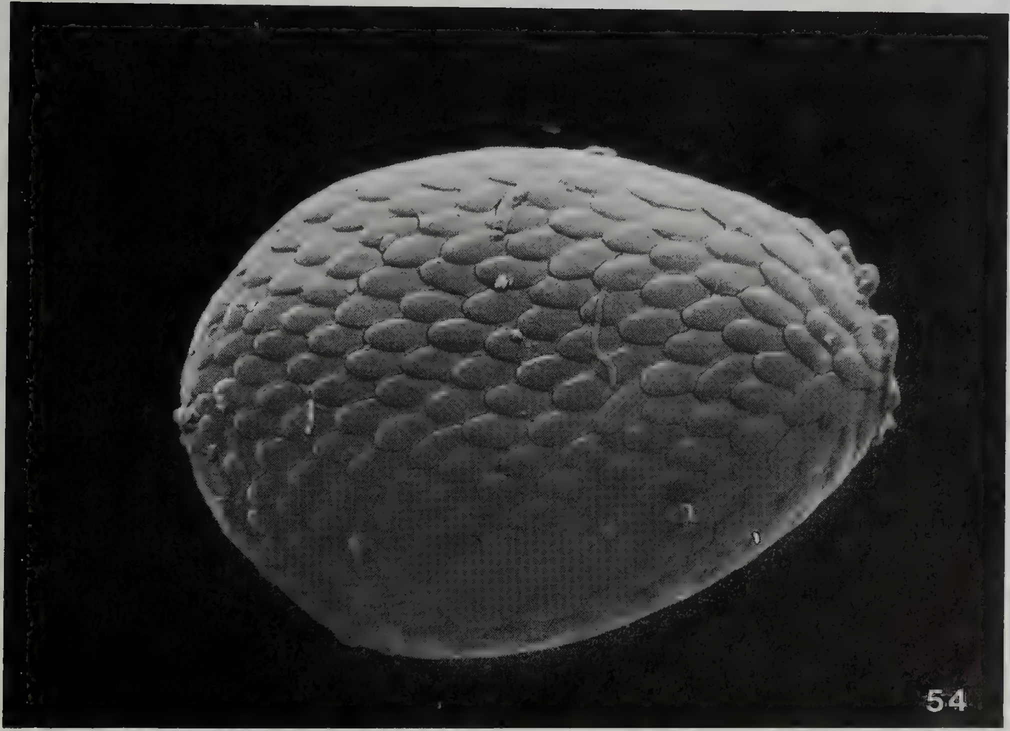

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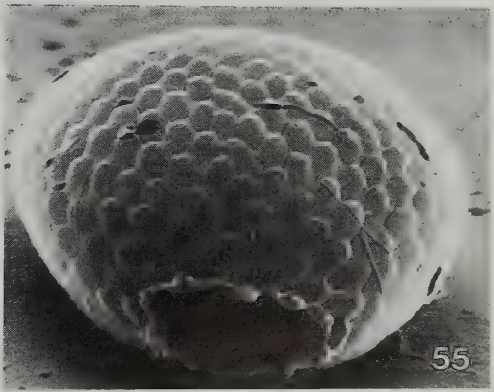

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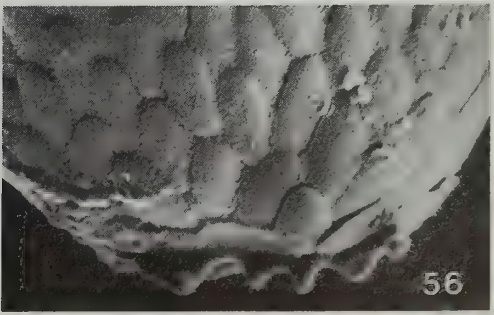

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Figs 51–56 ***Assulina muscorum***, light microscopic (Figs 51,52) and SEM-aspects (Figs 54–56) and ideal individual (Fig. 53). **51** Broad lateral view of atypically broad specimen. **52** Broad lateral view of typic specimen. **53** Broad lateral, narrow lateral and ventral view. **54,55** Broad lateral and ventral view, × 2100, × 1700. **56** Aperture showing organic cement, × 3400. Scale bar divisions 10 µm.

aperture and platelets show greater variability (Table 8). Cash & Hopkinson (1909) describe a maximum shell length of 30–38 µm, Grospietsch (1954) about 45 µm, Bonnet & Thomas (1960*a*) 30–35 µm and Decloitre (1961) 30–40 µm. The shell measurements of our population deviate slightly, being smaller (Table 8).

Strikingly often 2 differently sized individuals can be found united at their apertures. In most cases the larger of the two specimens contains a cyst (Fig. 43) which has, especially when older, a jagged cyst wall. This phenomenon, which is frequent among all members of the genus *Paraquadrula*, has been reported by many authors (Penard, 1902; Deflandre, 1932; Gauthier-Lièvre, 1953; Schönborn, 1965) and might be interpreted as a form of sexuality (see Figs 45–50). Although sexual processes have been described for some testacean species, they are poorly documented. Some authors reported conjugation, followed by encystation, but did not observe nuclear fusion (Penard, 1902; Awerintzew, 1907; Cash & Hopkinson, 1909; Pateff, 1926; Deflandre, 1932; Chardez, 1960), e.g. the cysts contained 2 nuclei.

It is evident from protargol silver impregnated specimens of *P. irregularis* that nuclear fusion takes place. Figures 45–50 document the following steps: A cell divides into 2 daughter cells (Fig. 45; this stage occurred in 5.5% of 200 investigated specimes = 100%), each having a nucleus with central nucleolus (Fig. 46; 11%); the plasma of 2 cells fuse (Fig. 47; 12%); the 2 nuclei fuse (Figs 48,49; 14.5%), followed by the fusion of their nucleoli (Fig. 50; 17%); a cyst is formed (Figs 42,50). Without doubt, the processes photographed in Figs 47–50 show fusions of 2 cells and not binary fissions, since the shells of the united specimens are complete, and even food residues of the former cells are easily to be seen in the abandoned shells (cp. Fig. 45, representing binary fission).

Unfortunately, we could not follow these processes in living specimens; thus it is unclear, whether the uniting cells are parent and daughter or are from 2 different specimens, which would be a true conjugation. The former suggestion is confirmed by Schönborn (1965), who documented a reunion of parent and daughter cells without nuclear fusion, speculating that this phenomenon is caused by formation of an undersized daughter test. However, we also found cysts in smaller or equal sized shells. Such cases have been attributed to plasmogamy by Schönborn (1965). On the other hand, Pateff (1926) and Deflandre (1932) described copulation of strikingly different sized specimens in *Difflugia mammillaris* and in *P. irregularis* (without nuclear fusion), and Penard (1902) reported for *Cryptodifflugia oviformis* that cysts are always formed in the smaller of the two tests.

Valkanov (1962*b*) has observed copulation of equal sized specimens in *P. madarica*, followed by nuclear fusion. He also provided photographic evidence of a syncaryon in *Euglyphella delicatula* (Valkanov 1962*a*, Abb. 1). Our figures 45–50 are, with exception of Valkanov's picture, the first photographic document of nuclear fusion in testate amoebae. Further investigations are needed to determine, whether autogamy takes place or not, and to follow the fate of the syncaryotic cysts.

For detailed ecological data of this species see Bonnet (1989*b*).

Assulina muscorum Greeff, 1888

Figs 51–56, Tables 1,9

BM (NH) Reg. No. 1990.4.26.8

Young shells yellowish, older ones light to dark brown, compressed, composed of elliptic, sometimes irregularly arranged platelets. Aperture terminal, elliptic, with more or less pronounced collar of organic cement (Fig. 56; cp. Ogden & Hedley, 1980; Ogden, 1981, 1984). Collar distinctly lobed, contrary to *A. collaris*, Kufferath, 1932, which is, in our opinion, a doubtful species—but see Schönborn & Peschke (1988).

Parameters (1) and (3) fairly constant (CV 8.3 and 8.5), variability of characters (4) and (5) relatively high (CV 17.5 and 23.3; Table 9). The data of Cash et al. (1915) correspond with ours, while those of Ogden & Hedley (1980) and Ogden (1984) are moderately higher. Hoogenraad & De Groot (1937) studied different populations of *A. muscorum*, of which the so-called 'Middel'-population (Fig. 4 of Hoogenraad & De Groot, 1937) matches our population well. This is also true for the Thuringian population analyzed biometrically by Schönborn & Peschke (1988), despite the great geographic distance! Even the coefficient of variation of each single character coincides strikingly well.

Corythion asperulum Schönborn, 1988 in Schönborn & Peschke, 1988

Figs 57–62, Tables 1,10

BM (NH) Reg. No. 1990.4.26.2.

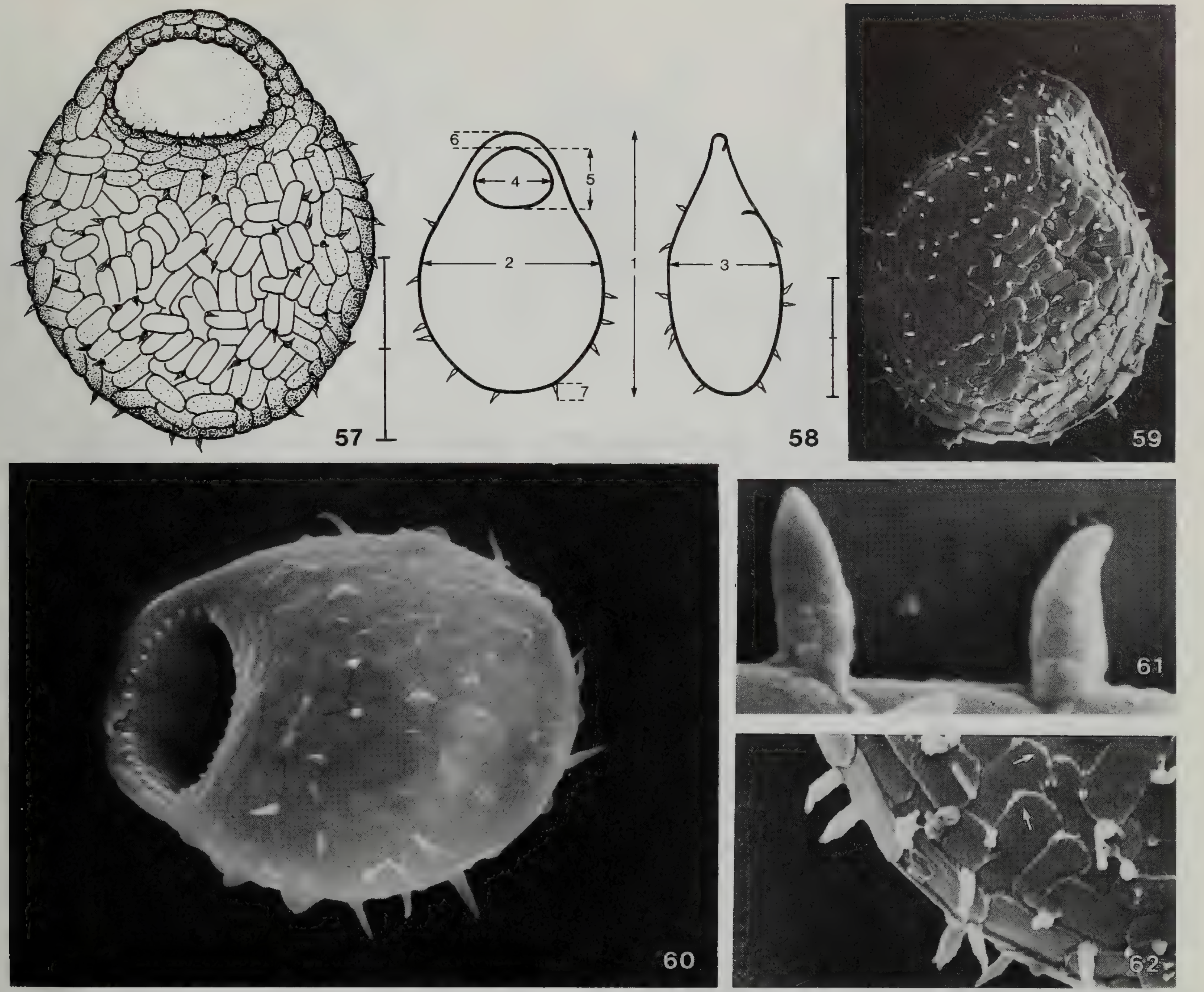
Shell colourless, ovoid, flattened, composed of irregularly arranged elliptic shell platelets (Fig. 57). Numerous about 3 µm long, siliceous, 'flame-like' spines projecting from junctions of idiosomes over entire shell except in apertural region (Figs 60,61). Organic cement plentiful, can be seen as small border surrounding each platelet (Fig. 62). Separation from the very similar *C. dubium* var. *spicatum* by means of the spines, which are longer, in 1 single row and consist of chitin in *C. dubium* var. *spicatum*.

Table 10. Morphometric characterization of *Corythion asperulum*. All measurements in µm.

Character	x̄	M	SD	SE	CV	Min	Max	n
(1)	44.7	45.0	3.9	1.03	8.7	32	48	14
(2)	32.7	32.0	3.3	0.92	10.1	23	36	13
(3)	18.9	19.0	3.0	0.87	16.0	13	22	12
(4)	14.0	14.0	2.3	0.63	16.2	8	16	13
(5)	10.6	10.0	1.9	0.51	17.4	6	13	13
(6)	3.2	3.0	0.9	0.24	27.3	2	5	13
(7)	3.0	3.0	0.7	0.19	22.7	2	4	13

Table 11. Morphometric characterization of *Euglypha compressa*. All measurements in µm.

Character	x̄	M	SD	SE	CV	Min	Max	n
(1)	87.4	88.5	10.8	2.42	12.4	65	115	20
(2)	61.2	61.0	7.0	1.56	11.4	50	76	20
(3)	32.4	33.0	2.6	0.97	7.9	29	35	7
(4)	24.2	24.0	3.4	0.76	14.1	18	32	20
(5)	14.6	14.0	2.8	1.07	19.4	10	19	7
(6)	8.0	8.0	0.9	0.23	11.8	6.5	10	16
(7)	22.1	22.0	3.3	0.78	15.0	16	29	18
(8)	8.1	8.0	1.5	0.36	18.3	6	11	17
(9)	4.6	4.0	1.2	0.29	25.6	3	7	17



Figs 57–62 ***Corythion asperulum***, light microscopic (Fig. 57) and SEM-aspects (Figs 59–62) and ideal individual (Fig. 58). **57** Ventral view. **58** Ventral and lateral view. **59,60** Dorsal and ventral view, × 1200, × 1700. **61** Spines, × 12300. **62** Detail of surface, × 3200. Note organic cement surrounding platelets (arrows). Scale bar divisions 10 µm.

Shell measurements show rather high variability; only parameter (1) has a CV less than 10% (Table 10). The biometric data of Schönborn & Peschke (1988) correspond almost perfectly to our own, despite the extreme geographic distance. Only character (3) shows a slightly higher variability in our population. Schönborn & Peschke (1988) did not mention the organic cement surrounding the platelets (Fig. 62).

As far as we know, this is the the first record since the original description, and especially remarkable, being from Australia!

Euglypha compressa Carter, 1864

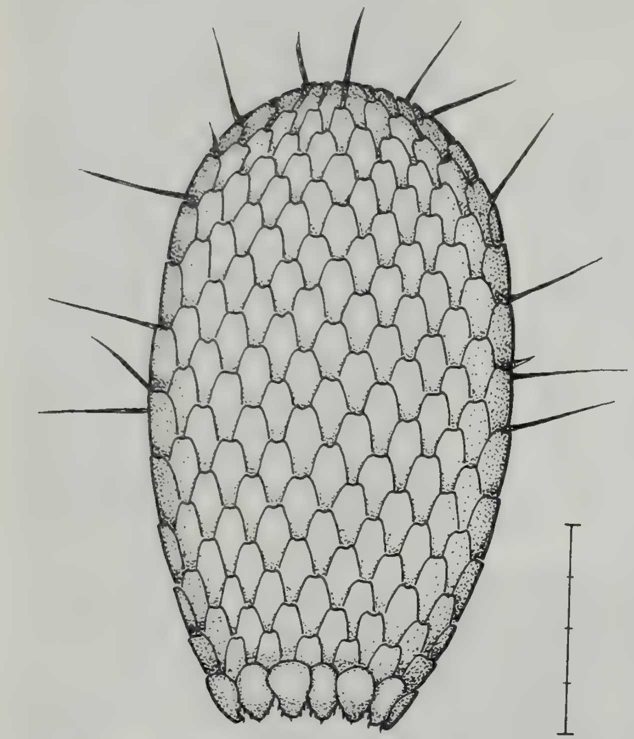
Figs 63–68, Tables 1,11

BM (NH) Reg. No. 1990.4.26.1

Shell colourless, obovoid, compressed 2:1, composed of about 300 platelets (often with notched narrow side; Fig. 68). Several 16–19 µm long spines projecting singly from junctions of shell platelets close to lateral margins (Fig. 66). Aperture elliptic, about 15 apertural platelets. Platelets thickened at denticulate margins, carrying 1 large median tooth. Presumably always 3 pairs of lateral teeth, of which only 2 are easy to see; third is bent inward at right-angles to apertural opening, very small and thus difficult to recognize (Fig. 67).

Shell measurements moderately varying (Table 11), corresponding well with those of Wailes & Penard (1911), Cash et al. (1915) and Ogden & Hedley (1980). The values of Carter (1864) are slightly higher, those of Ogden (1981) lower (61–75 µm length; n = 31).

The peculiar notching of the idiosomes, which give the platelets a hexagonal appearance (Penard, 1902; Cash et al., 1915) is also evident in the scanning electron micrographs of Ogden & Hedley (1980), Ogden (1981) and Rauenbusch (1987, for *E. compressa* var. *glabra*). The drawings in Cash et al. (1915) show 5 different types of spines. Ogden (1981) also emphasizes that 2 types exist within this species. The spines of



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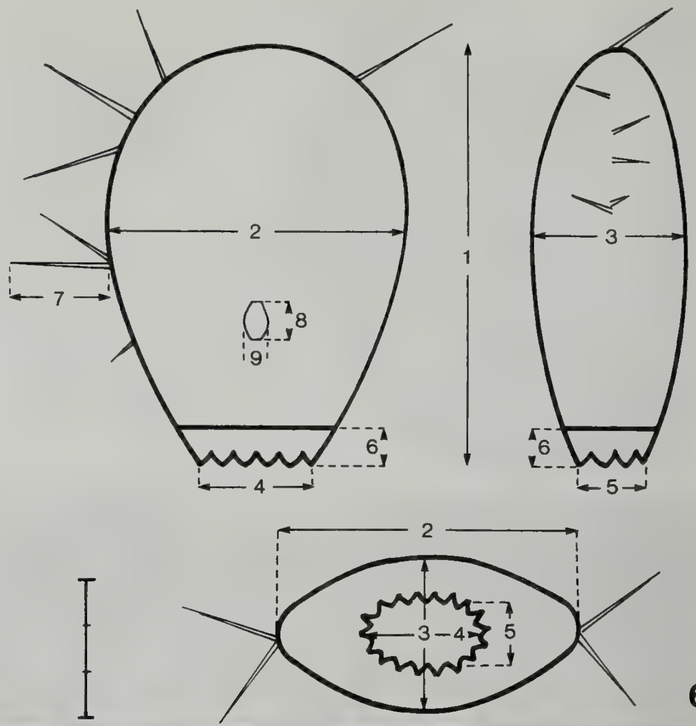

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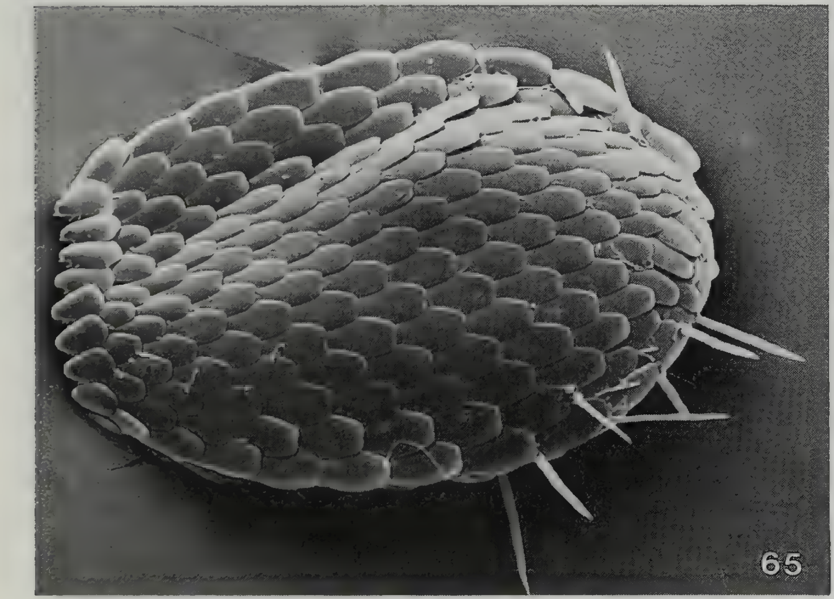

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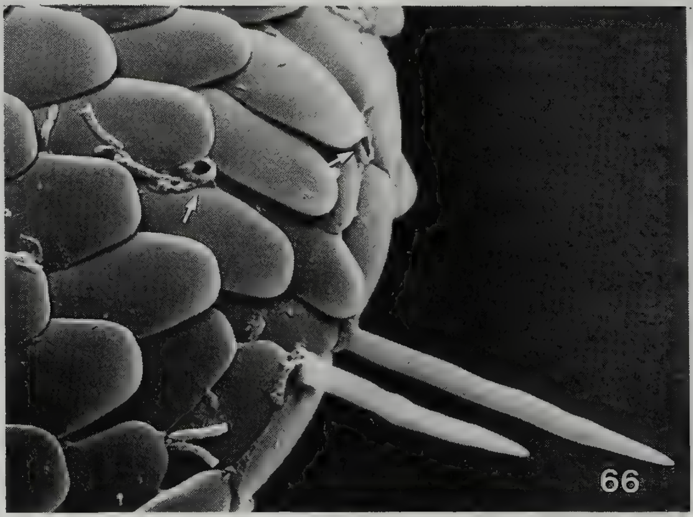

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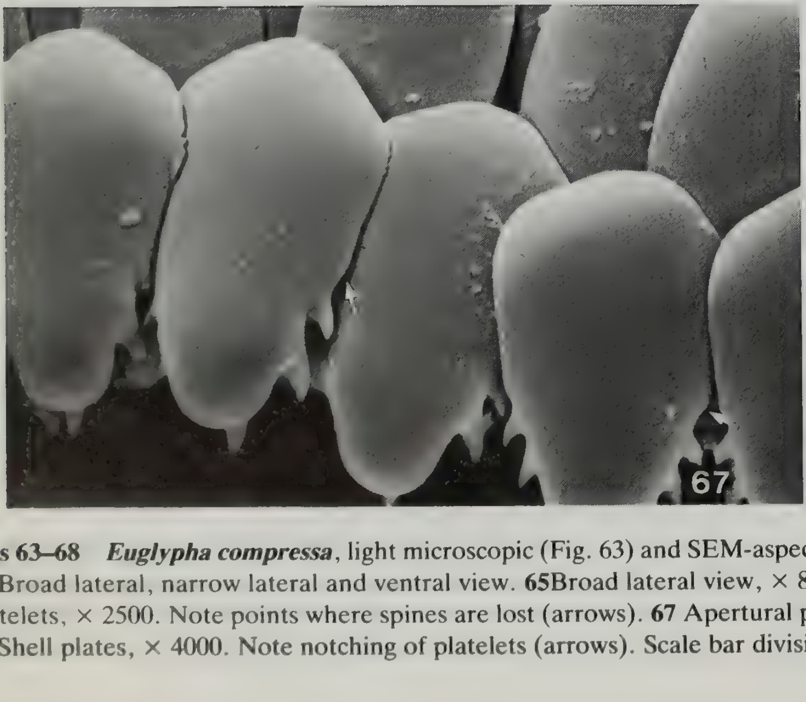

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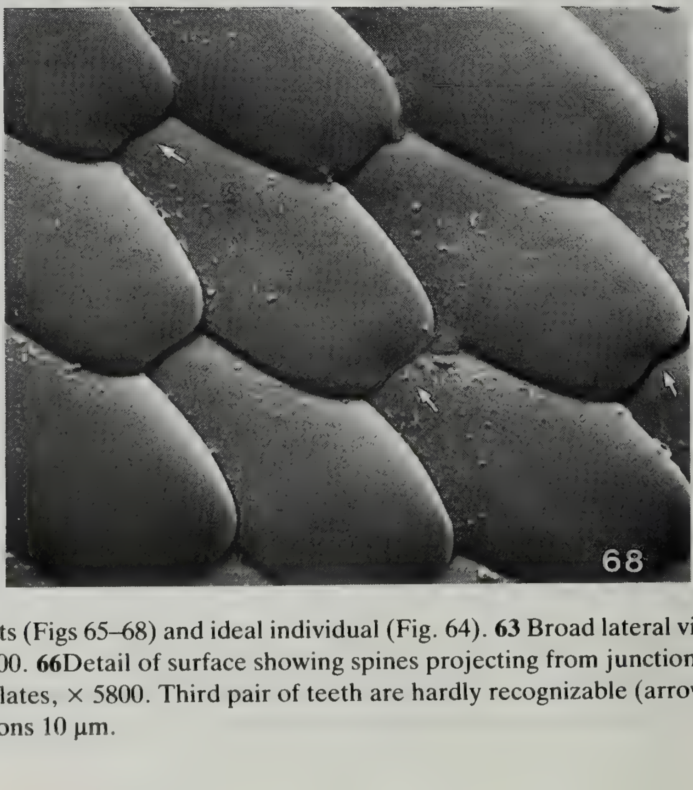

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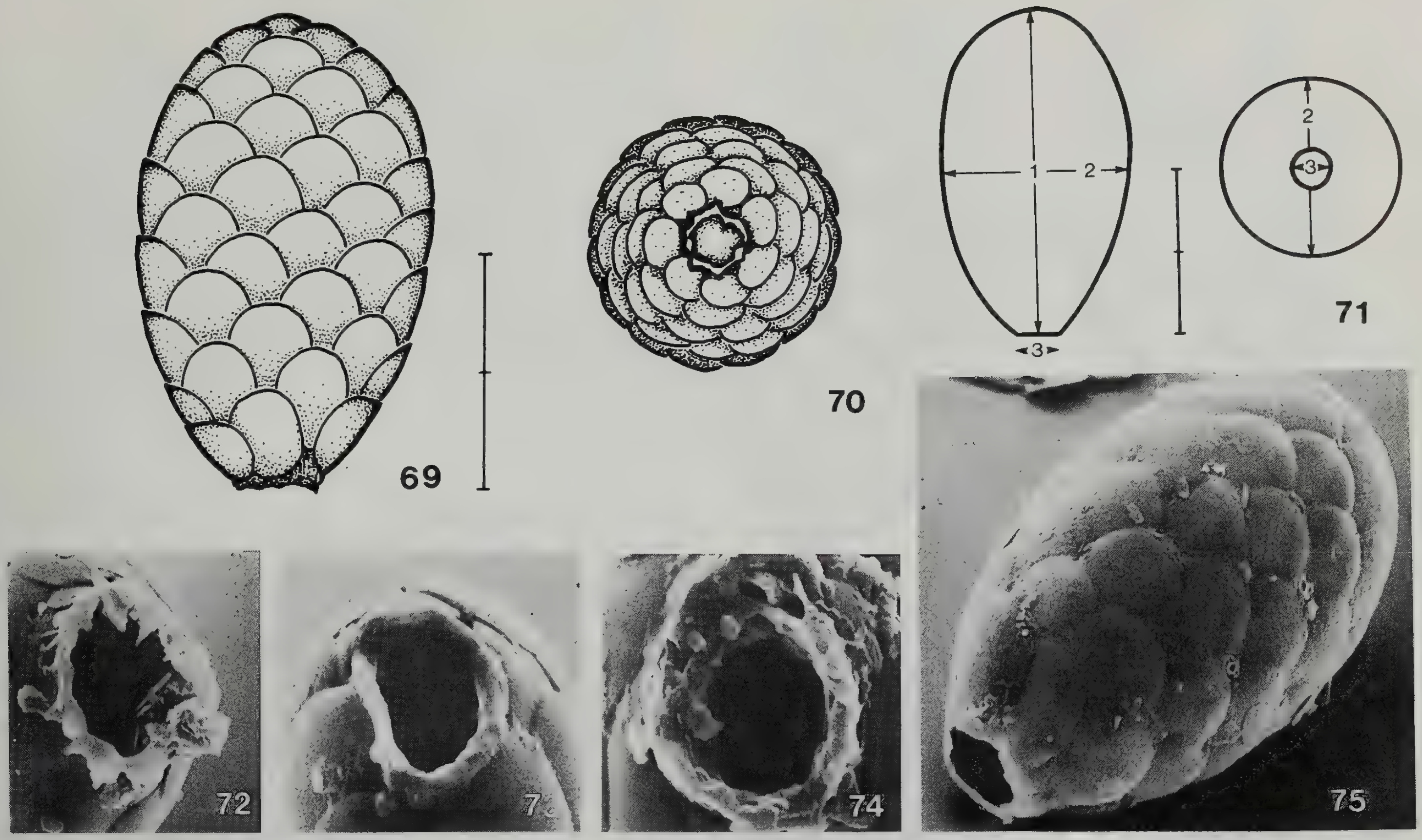
Figs 63–68 ***Euglypha compressa***, light microscopic (Fig. 63) and SEM-aspects (Figs 65–68) and ideal individual (Fig. 64). **63** Broad lateral view. **64** Broad lateral, narrow lateral and ventral view. **65**Broad lateral view, × 800. **66**Detail of surface showing spines projecting from junctions of platelets, × 2500. Note points where spines are lost (arrows). **67** Apertural plates, × 5800. Third pair of teeth are hardly recognizable (arrows). **68** Shell plates, × 4000. Note notching of platelets (arrows). Scale bar divisions 10 µm.



Figs 69–75 ***Tracheleuglypha dentata***, light microscopic (Figs 69,70) and SEM-aspects (Figs 72–75) and ideal individual (Fig. 71). **69–71** Lateral and ventral views. **72–74** Apertures with differently shaped collars, × 3800, × 3900, × 4200. **75** Ventro-lateral view of specimen without distinct collar, × 1500. Scale bar divisions 10μm.

our population represent the type photographed in Pl. 78 of Ogden & Hedley (1980). Presumably such populations should be separated at species level.

Tracheleuglypha dentata (Penard, 1890) Deflandre, 1928

Figs 69–75, Tables 1,12

BM (NH) Reg. No. 1990.4.26.3

Shell colourless, obovoid, circular in transverse section, composed of about 100 circular, regularly overlapping platelets, usually about 7 μm in diameter (often smaller in apertural region). Circular aperture terminal, usually, but not always, surrounded by chitinous collar (Figs 72–75).

Coefficients of variation are between 11.3 and 17.5%. Character (3) and diameter of shell platelets show the greatest variability (Table 12). Our measurements correlate well with those of Penard (1890, 1902), Cash et al. (1915), Thomas & Gauthier-Lièvre (1959) and Rauenbusch (1987), whereas the population of Ogden & Hedley (1980) is slightly larger. A comparison of our values with the average values (1 free-living and 3 cultivated populations combined) of Ogden & Coûteaux (1987) shows a high conformity, even in standard deviations. The measurements for *T. acolla*, given by Bonnet & Thomas (1955), also agree with ours.

As already mentioned, specimens of our population may or may not have a collar. Traditionally, individuals without collar are considered as a separate species, *T. acolla* (Bonnet & Thomas, 1955). The transitions between individuals with and without collar are manifold and have indeed been documented by numerous authors using scanning electron microscopy. Thus, Fig. 6 in Ogden & Coûteaux (1987), Pl. 34 Fig. a in Rauenbusch (1987) or Pl. 90 Fig. B in Ogden & Hedley (1980), which are described as *T. dentata*, correspond with the scanning electron micrographs of *T. acolla* in Bonnet (1975), Grospietsch (1982) and Chardez & Rassel (1985). Ogden & Coûteaux (1987, 1988), however, suggest that the collar serves in holding parent and daughter cells together during division, and may be absent, especially in empty shells taken from field samples (presumably by natural causes such as predation or influence of bacteria).

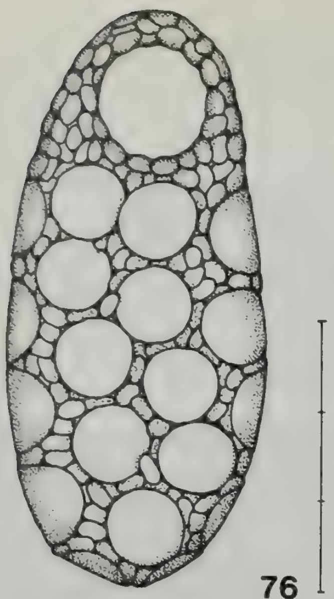
The larger shell platelets of *T. acolla* are considered an additional criterium in separating it from *T. dentata* (Bonnet & Thomas, 1955). However, Chardez (1960) found 4 different types of platelets in various populations of *T. acolla*. Our population matches the type with large (about 9 μm) circular platelets (Fig. 75). Regarding the drawings of Bonnet & Thomas (1960*a*), which unfortunately do not give measurements for the diameters of platelets, it is evident that the platelets of their species designated as *T. acolla* have a maximum diameter of 5 μm. This is even smaller than in our population. These data strongly suggest synonymy of *T. dentata* and *T. acolla* as already indicated by Ogden & Coûteaux (1987).

Trinema enchelys (Ehrenberg, 1838) Leidy, 1878

Figs 76–83, Tables 1,13

BM (NH) Reg. No. 1990.4.26.4

Shell colourless, elliptic, almost circular in transverse section, composed of about 60 circular, scarcely overlapping large platelets. Many smaller, different sized platelets fill space between large ones (Fig. 83). Aperture circular, invaginated, surrounded by 2 rows of small idiosomes and about 30



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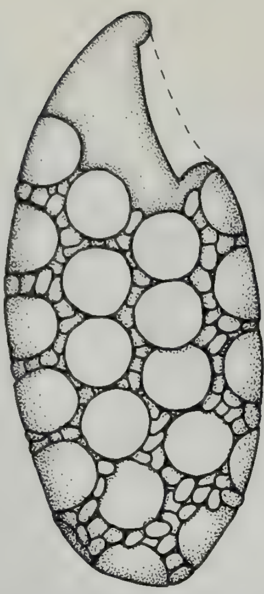

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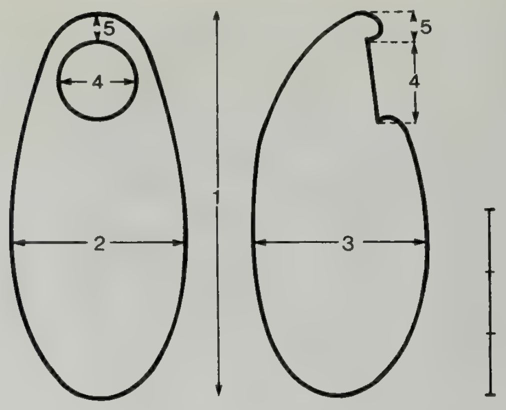

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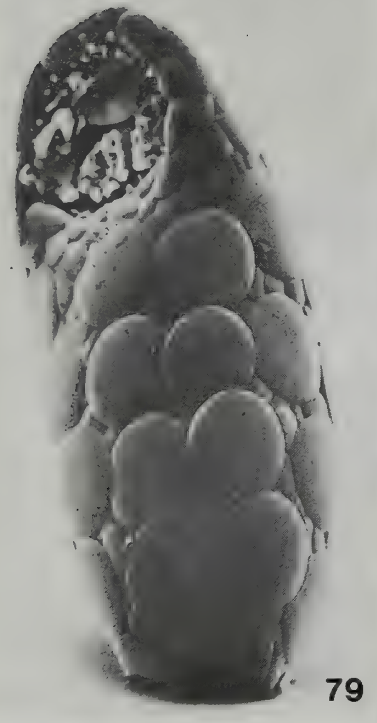

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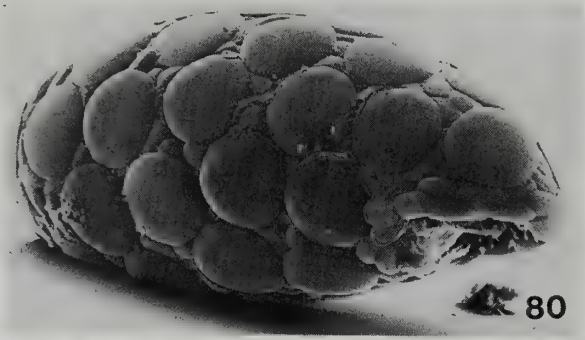

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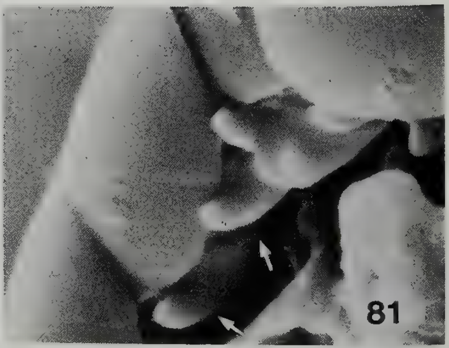

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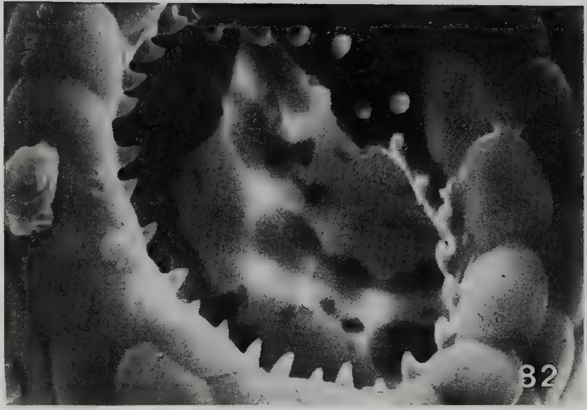

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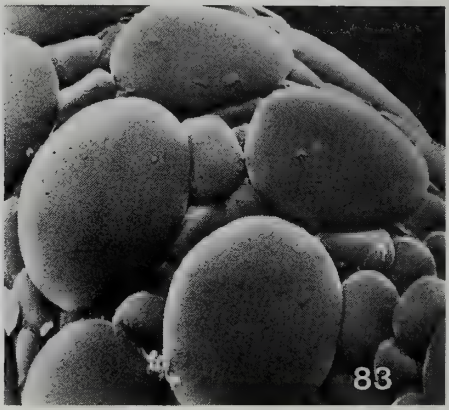

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Figs 76–83 ***Trinema enchelys***, light microscopic (Figs 76,77) and SEM-aspects (Figs 79–83) and ideal individual (Fig. 78). **76–78** Ventral and lateral views. **79,80** Ventral and lateral view, × 1400, × 1000. **81** Apertural platelets (arrows), × 6500. **82** Aperture, × 3500. **83** Detail of surface, × 2500. Scale bar divisions 10 μm.

Table 12. Morphometric characterization of *Tracheleuglypha dentata*. All measurements in μm.

Character	x̄	M	SD	SE	CV	Min	Max	n
(1)	41.1	40.0	4.7	0.92	11.3	35	51	26
(2)	23.2	22.0	2.8	0.55	12.0	19	29	26
(3)	6.2	6.0	1.0	0.21	16.5	5	8	26
Platelets, diameter	6.7	8.0	1.2	0.23	17.5	5	9	25

apertural platelets, each having 1 median tooth (Figs 81,82).

Coefficients of variation of characters (1)–(3) are less than

Table 13. Morphometric characterization of *Trinema enchelys*. All measurements in μm.

Character	x̄	M	SD	SE	CV	Min	Max	n
(1)	64.3	63.0	5.7	1.51	8.8	58	74	14
(2)	27.9	28.5	2.8	0.74	9.9	23	32	14
(3)	28.5	28.0	2.6	0.71	9.0	25	32	13
(4)	12.3	13.0	1.4	0.37	11.3	10	15	14
(5)	4.9	5.0	0.8	0.21	15.9	4	6	14
Great platelets, diameter	8.6	8.5	1.3	0.36	15.7	7	11	14

10%, others have greater variability (Table 13). The populations investigated by Lüftenegger et al. (1988*a*) are considerably smaller (< 50 µm), but the coefficients of variation—especially those of the (PII)—agree quite well with the new data (Table 13). The high interpopulation variability of *T. enchelys* (Chardez, 1956) is evident from data in the literature, ranging all the way from 40 µm to 140 µm (Hoogenraad & De Groot, 1940; Rauenbusch, 1987). However, its usual size is 50–60 µm, which agrees well with our own data and with those of Ogden & Hedley (1980).

Shell shape and shape and arrangement of platelets are very similar in all populations investigated with the scanning electron microscope (Ogden & Hedley, 1980; Rauenbusch, 1987; Figs 79–83).

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A revision of *Cothurnia* (Ciliophora: Peritrichida) and its morphological relatives

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Synopsis. The loricate peritrich genera *Cothurnia*, *Cothurniopsis*, *Cyclodonta* and *Dimorphocothurnia* are revised and a key to the constituent species of each is given. Several species are synonymised or transferred to other genera and one, *Cothurnia felinska*, is erected. Four closely related genera, *Baikalotheca*, *Semicothurnia*, *Tesnotheca* and *Daurotheca* are discussed. All extant species are described and figured.

INTRODUCTION

In recent years four genera belonging to the family Vaginicolidae have been taxonomically revised, namely *Pyxicola* (Trueba, 1978), *Thuricola* and *Pseudothuricola* (Trueba, 1980), and *Platycola* (Warren, 1982). The present publication aims to extend the revision of the Vaginicolidae to those genera in which the loricas are held erect on an external stalk, and which lack a special valve or possess only a simple means of closing the aperture (*Cothurniopsis*). The major genus dealt with here is *Cothurnia* Ehrenberg, 1831, a well known genus that contains a large number of nominal species. Many species of *Cothurnia* have previously been transferred to other genera but until recently no check list of those remaining was available, thus making it difficult for the taxonomist and ecologist to identify them. In this paper *Cothurnia* and three other closely related genera, *Cothurniopsis*, *Cyclodonta* and *Dimorphocothurnia*, are taxonomically revised. A key to species and a check list of nominal and extant species of each genus are also provided.

GENERAL MORPHOLOGY AND TAXONOMIC CHARACTERS

Morphology

Accounts of the biology and morphology of genera belonging to the family Vaginicolidae were given by Kralik (1961), Trueba (1978, 1980) and Warren (1982), so it is sufficient here to give a short summary highlighting those features common to the cothurnids.

Figure 1 shows the main morphological features of a typical species of *Cothurnia*. It consists of a lorica which has an aperture at the anterior end, a stalk at the posterior end and contains either one or two zooids. The zooids are typically cylindrical or trumpet-shaped and when relaxed may extend far beyond the aperture, but when contracted withdraw completely within the lorica. Zooids are attached to the base of the lorica either directly by means of one or two non-contractile stalks, or by a series of membranes (e.g. *Cyclodonta*).

The lorica is attached to its substrate by a non-contractile external stalk. In many species the stalk appears to be smooth and comparatively featureless, while others possess lines or stripes which run longitudinally down the stalk. Stalks possessing such stripes have been described as 'fibrillar' (Felinska, 1965) or 'striated' (Lang, 1948). Examination by TEM reveals that the stalk is bounded by an outer limiting membrane and contains tubules arranged in cylindrical groups ('Tubular Units') within a microfibrillar matrix (Vogelbein and Thune, 1988). This is broadly consistent with the findings of Randall and Hopkins (1962) who reported that the longitudinal stripes observed in the non-contractile stalks of aloricate peritrichs are also due to tubular structures in the stalk matrix. In this revision, these lines shall be referred to as longitudinal striae. Transverse folds or furrows may also be present on the stalk surface. In some species the external stalk penetrates the lorica wall via a special tube at the posterior end (Banina and

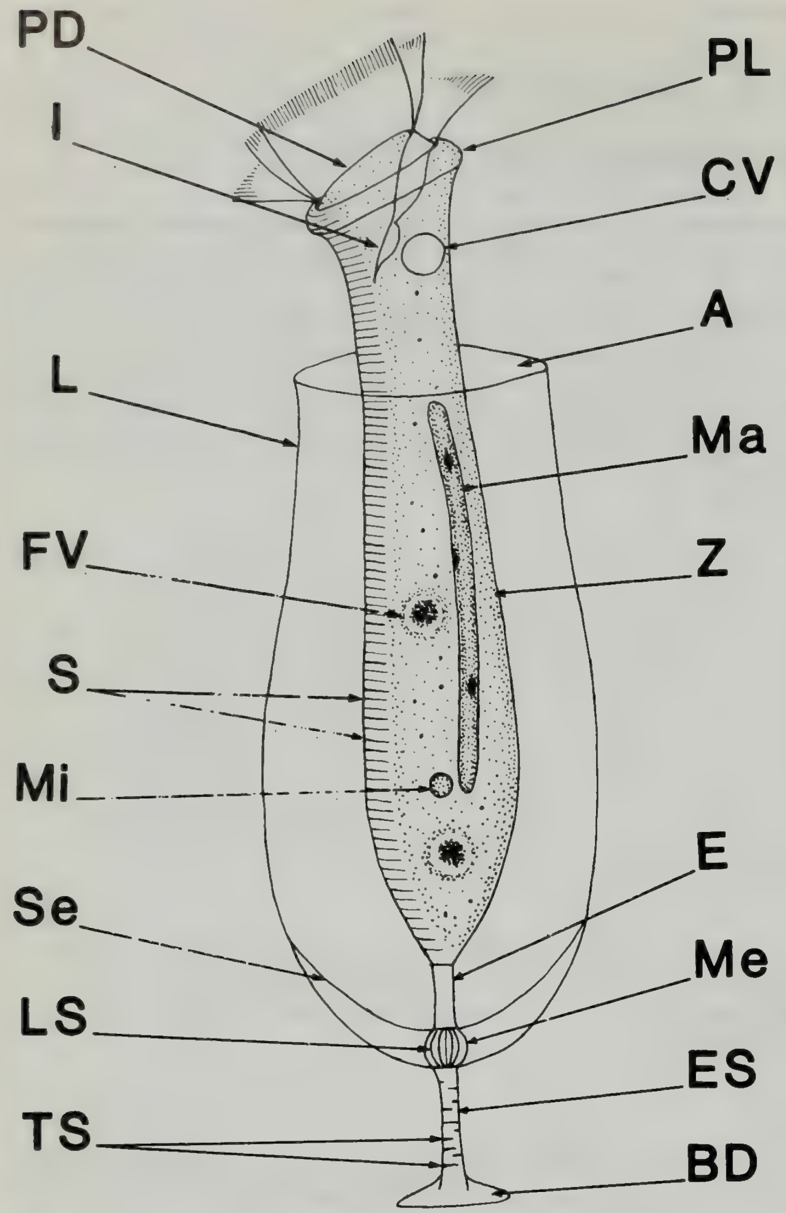


Fig. 1 A generalised *Cothurnia* showing the principal morphological features. A—aperture; BD—basal disc; CV—contractile vacuole; E—endostyle; ES—external stalk; FV—food vacuole; I—infundibulum; L—lorica; LS—longitudinal striae; Ma—macronucleus; Me—mesostyle; Mi—micronucleus; PD—peristomial disc; PL—peristomial lip; S—striations; Se—septum; TS—transverse striae/folds; Z—zooid.

Polyakova, 1977). No tube was observed by Vogelbein and Thune (1988).

At its point of attachment to the substrate the stalk is flared forming the basal disc. The basal disc rests on a layer of adhesive material which extends up to 10μm beyond the disc edge. The adhesive is thought to be secreted during the process of attachment to the substrate (Vogelbein and Thune, 1988).

In many cothurnids the lorica contains an extra layer of material forming an internal lining or septum. The septum is most easily seen in the posterior region where it encloses a space at the base of the lorica. In these cases, the zooid is attached to the base of the lorica via a non-contractile middle stalk or 'mesostyle'. The mesostyle is usually short and broad with conspicuous longitudinal striae. Another stalk, the endostyle, may also be present and connects the zooid either to the lorica or (when present) to the septum. The endostyle is usually short and slender.

Except in *Cothurniopsis*, there is no mechanism of closing the aperture of the cothurnid lorica. In *Cothurniopsis* the border of the aperture is pliable and folds in to close the aperture when the zooid contracts. According to Stokes (1893) there do not appear to be any special structures involved, but rather the border closes passively as a result of the contraction of the zooid. The precise mechanism by which the aperture closes has yet to be elucidated and is therefore considered a doubtful generic character. Nevertheless, until a redescription is available, *Cothurniopsis* remains a separate genus.

Cothurnids are found in fresh, brackish and marine waters and have a cosmopolitan distribution. They have been recorded on plant, animal (commonly as epizoites of Crustacea) and inanimate substrates. They are not generally regarded as parasitic *sensu stricta*.

Taxonomic characters

Like most other peritrich groups, it is comparatively easy to characterise cothurnid genera but difficult to identify individual species. Many species have only been described once and, in some cases, descriptions were based on poorly fixed or unhealthy specimens. Consequently, important taxonomic data are unavailable for several taxa. The characters used as a basis for this revision are as follows.

Lorica shape

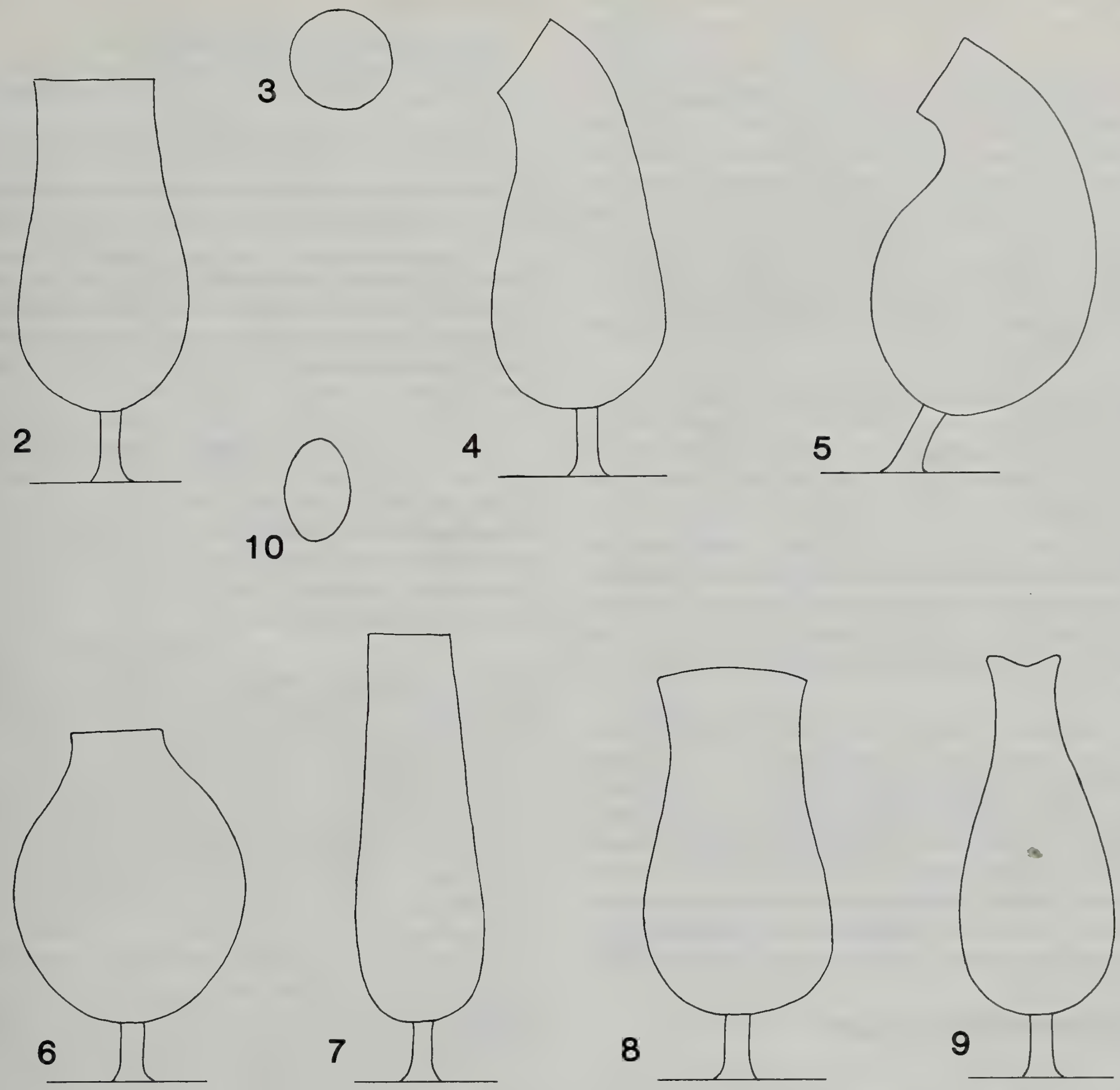
The dominant feature used for classifying cothurnids, and indeed vaginicolids in general, is the shape of the lorica. Identification keys published by Kahl (1935), Wailes (1943) and Stiller (1971) rely extensively on lorica shape for separating species. Two advantages of the lorica are, (i) it is unaffected by fixation or other methods of preservation, and (ii) it has been described for every known species. Nevertheless, opinions differ over the usefulness of lorica shape as a taxonomic character since variability is well documented (Kralik, 1961; Trueba, 1980; Warren, 1982).

The cothurnid lorica is typically cylindrical in shape with a rounded, often bulbous posterior end (Fig. 2). There is an aperture at the anterior end that is circular when viewed from above (Fig. 3). One or more clefts may be present in the aperture border. The main lorica axis is normal to the substratum and extends in straight line from the point of attachment to the external stalk. The aperture is usually at right angles to the main lorica axis although in some cases the neck just below the aperture is curved tilting the aperture obliquely to the main lorica axis (Fig. 4). Occasionally, the whole lorica may be curved (Fig. 5).

The lorica may be, (i) compressed or elongated along the main lorica axis resulting in oblate (Fig. 6) or prolate (Fig. 7) forms, or (ii) compressed in a plane at right angles to the main lorica axis (Figs 8 & 9) producing dorso-ventral flattening (Precht, 1935). Variations of the first type are readily observed, but dorso-ventral compression becomes apparent only if the lorica is viewed either from above, or from both the dorso-ventral and lateral aspects (Fig. 10). Most descriptions of cothurnids are based on observations from one direction only. Yet with all its limitations, the shape of the lorica remains a useful taxonomic character.

Lorica size

The dimensions most commonly used in species diagnoses are lorica length, maximum lorica width, and width of the



Variations in shape of cothurnid loricas (following the terminology of Precht, 1935). **Fig. 2** Normal lorica. **Fig. 3** Normal aperture viewed from above. **Fig. 4** Lorica with a curved neck. **Fig. 5** Curved lorica. **Fig. 6** Oblate lorica. **Fig. 7** Prolate lorica. **Figs 8–10** Dorso-ventrally compressed lorica, fig. 8 ventral view, fig. 9 lateral view, fig. 10 aperture viewed from above.

aperture. Ideally several individuals should be measured and the range of variation given. Among other peritrichs it has been suggested that the ratio of length: width is a more meaningful character than size alone (see Warren, 1987), and this may also prove to be the case for cothurnid loricas.

Stalks

All cothurnids possess a non-contractile external stalk attaching the lorica to the substratum. Some authors (Entz, 1884; Jankowski, 1985) have suggested that the size of the stalk and the presence of transverse folds on its surface are generic characters. In this revision stalk size and surface folding are not employed at the generic level although they are used for separating species. A few species appear to have a special tube at the posterior end of the lorica through which the external stalk penetrates the lorica wall (Banina and Polyakova, 1977).

Mesostyles and endostyles are frequently included in descriptions of cothurnids and have long been recognised as useful characters for separating species. Jankowski (1985) suggested that the presence or absence of mesostyles and endostyles should be regarded as generic characters although acceptance of this decision must await further studies.

Zooids

The taxonomy of aloricate peritrichs is based largely on characters relating to the zooid (Foissner, 1981; Warren, 1987), frequently omitted from species descriptions of cothurnids. Descriptions available are often from studies made on fixed, contracted cells yielding information of limited value. The following zooid characters are useful; size and shape of zooid, peristomial lip, disc and macronucleus; position within zooid of contractile vacuole; number and spacing of pellicular striations. However, the following points should be noted with reference to these characters.

i) Zooid size; the proportion of the total zooid length which extends beyond the aperture may be more significant than size alone.

ii) Size and shape of peristomial lip and disc. Felinska (1965) suggested that the shape of the disc is an important taxonomic character since it 'has no transitory forms and does not undergo modifications', and divided thirteen species of *Cothurnia* into two groups—those with convex discs and those with flat, oblique discs. While the shape of the disc is probably a useful character in healthy peritrichs it should be noted that, among aloricate forms at least, the shape of the disc varies in response to changes in environmental conditions (see Warren, 1987).

iii) Position within zooid of contractile vacuole (CV). The CV often lies either in or just below the peristomial region although in some descriptions its position is described in relation to the infundibulum. If, however, the infundibulum is short or orientated obliquely, differences may be subtle.

iv) Size and shape of macronucleus. Entz (1884) cited the shape of the macronucleus as one of the principal differences between *Cothurnopsis* (compact macronucleus) and *Cothurnia* (band-like or vermiform macronucleus). In this revision the macronucleus is employed as a taxonomic character at the species level only.

v) Pellicular striations. Biometric analysis of pellicular striations are used increasingly in the taxonomy of aloricate peritrichs (Foissner, 1979, 1981; Foissner and Schiffmann, 1974, 1975), although few studies of this type have been carried out on loricate peritrichs. Nevertheless it is usually possible to determine whether the striations are widely spaced (clearly visible) or narrow spaced (fine or inconspicuous), and whether the ribbing between the striations is convex, concave or normal (Foissner and Schiffmann, 1975).

Colony and pseudocolony formation

Among the vaginicolids there are typically either one or two zooids per lorica, although in some genera examples of three or even four zooids per lorica have been reported (Kralik, 1961). Jankowski (1985) suggested that the presence of more than one zooid in each lorica represents a colony, and that coloniality should be regarded as a generic character among loricate peritrichs in the same way as it is among the aloricates. Unfortunately, as Jankowski (1985) himself points out, usually no attempt is made to determine the number of zooids per lorica other than at the time of observation, so it is almost impossible to know whether species described in the literature as 'solitary' are in fact immature 'colonial' forms. Therefore, due to the paucity of data available, 'coloniality' (*sensu* Jankowski, 1985) is not recognised as a generic character in this revision, although it is employed for the separation of species.

At least two species of *Cothurnia* (*C. bavarica* and *C. variabilis*) form pseudocolonies; that is they develop as chains with each individual attached to the lorica of its neighbour via its external stalk. A third species, *C. nebaliae*, also forms pseudocolonies and, in addition, exhibits a dimorphic lorica structure with the individual in contact with the substratum ('basont' Jankowski, 1985) having a substantially longer external stalk than the others in the chain. Jankowski (1980) erected the genus *Dimorphocothurnia* for *Cothurnia nebaliae* on the basis of its lorica dimorphism.

Key to genera

1 Aperture border rigid; no closure of aperture 2
Aperture border pliable, used to close aperture on contraction of zooid(s) .... ***COTHURNIOPSIS***

2 Zooid(s) attached to inside of lorica either directly or via stalk 3
Zooid(s) attached to inside of lorica via series of membranes .... ***CYCLODONTA***

3 Forms pseudocolonies; lorica dimorphism with individual in contact with substratum having longer external stalk than those of rest of chain .... ***DIMORPHOCOTHURNIA***
Usually does not form pseudocolonies; not exhibiting lorica dimorphism .... ***COTHURNIA***

Genus ***COTHURNIA*** Ehrenberg, 1831

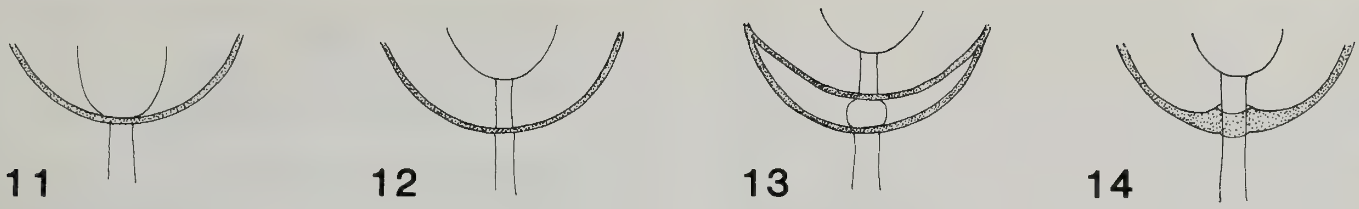
Cothurniopsis sensu Penard, 1914
Cothurnopsis Entz, 1884
Semicothurnia Jankowski, 1976
Sincothurnia Jankowski, 1985
Tesnotheca Jankowski, 1985

The name *Cothurnia* was first mentioned by Ehrenberg (in Hemprich & Ehrenberg, 1828) as part of an identification table in which loricate peritrichs with stalks (*Cothurnia*) were separated from those without stalks (*Vaginicola*). The original diagnosis of *Cothurnia* was founded on the description of *Cothurnia imberbis* Ehrenberg, 1831. A second species (*C. ? mystacina* Ehrenberg, 1831) was described at the same time but subsequently transferred to the genus *Acineta* (Ehrenberg, 1833). *C. imberbis* thus became the type species by monotypy. In his discussion of *Cothurnia*, Jankowski (1985) states that it is 'highly undesirable' for *C. imberbis* to be the type species because it is a 'very difficult' and 'in practice unstudied' organism; in its place he designated *C. maritima* Ehrenberg, 1838 as the type species. Jankowski was apparently unaware of Bacon's (1968) extensive study of *C. imberbis*, as a result of which more is known about this than any other species of *Cothurnia*. *C. imberbis* may therefore be properly designated as the type species of *Cothurnia*.

The taxonomy of *Cothurnia* remained largely unchanged over the next fifty years although several new species were added to the genus. In 1884 Entz erected the genus *Cothurnopsis* for cothurnid species with large, transversely folded external stalks and compact macronuclei. Kahl (1935) later submerged *Cothurnopsis* (which he misspelt '*Cothurniopsis*') into the genus *Cothurnia*, a decision supported by Matthes (1958) but opposed by Jankowski (1985).

In a recent review of the cothurnids, Jankowski (1985) divided the species of *Cothurnia* into those with two zooids per lorica, i.e. 'colonial' (*Sincothurnia*), and those with a single zooid per lorica (*Cothurnia sensu stricta*). A third genus, *Dimorphocothurnia* Jankowski, 1985, was erected for cothurnids which form pseudocolonies and possess dimorphic loricas. For the reasons stated in the previous section the concept of coloniality as a generic character has not been applied in this revision so *Sincothurnia* is synonymised in the genus *Cothurnia*.

Other genera erected by Jankowski for 'aberrant' *Cothurnia* species include *Baikalotheca* Jankowski, 1985, *Tesnotheca* Jankowski, 1985, *Semicothurnia* Jankowski, 1976 and



Various junctions between stalk and lorica found in *Cothurnia* **Fig. 11** External stalk only. **Fig. 12** Endostyle and external stalk. **Fig. 13** Mesostyle, endostyle and external stalk. **Fig. 14** Endostyle and external stalk which penetrates the lorica wall via a special tube.

Daurotheca Jankowski, 1987. *Baikalotheca* does not possess a true external stalk and so falls outside the scope of this paper. The main distinguishing feature of *Tesnotheca* is its asymmetrical zooid, while that of *Semicothurnia* is its prominent and distinctive stalk; neither character is considered sufficient to separate the genera, so the species of *Tesnotheca* and *Semicothurnia* are transferred to *Cothurnia*.

Daurotheca is characterised by its unusual lorica shape and a tendency to form spines on the lorica wall. *Daurotheca* is of uncertain taxonomic status and is dealt with here under *Incertae Sedis*.

Diagnosis of *Cothurnia*

Marine, brackish or freshwater loricate peritrichs usually with one or two zooids per lorica. Lorica borne on stalk and attached to aquatic animals, plants or inanimate objects. Lorica without valves or other means of closing the aperture. Inner layer or septum sometimes present enclosing a space at posterior end of lorica; septum connected to base of lorica via mesostyle. Zooid(s) attached to base of lorica (or septum) directly or via endostyle.

Key to the species of *Cothurnia*

Although the number of zooids per lorica has been used in this key, this character should be applied only to fully developed individuals; a lorica with one zooid may be a partly developed 'colonial' (*sensu* Jankowski, 1985) species.

1 Endostyle and mesostyle absent 2
Endostyle and/or mesostyle present 25

2 Marine 3
Freshwater 10

3 Diameter of aperture ⩾ maximum lorica width 4
Diameter of aperture < maximum lorica width 6

4 Lorica with ridges or furrows 5
Lorica without ridges or furrows .... ***C. innata***

5 Lorica 35–40 μm long with annular ridge near posterior end .... ***C. amoyensis***
Lorica 50–60 μm long with two or more ridges and furrows on anterior half of lorica .... ***C. antarctica***

6 External stalk without transverse folds or striae 7
External stalk with transverse folds and striae .... ***C. subglobosa***

7 Zooids reach as far as or just beyond aperture 8
Zooids extend at least one third of their length beyond aperture 9

8 Lorica symmetrical with annular ridges; aperture border without clefts .... ***C. curvula***
Lorica asymmetrical and without ridges; lateral borders of aperture with distinct cleft(s) .... ***C. inclinans***

9 Macronucleus lies transversely in body; zooid extends up to half its length beyond aperture .... ***C. mobiusi***
Macronucleus lies longitudinally in body; zooid extends up to one third of its length beyond aperture .... ***C. ovalis***

10 External stalk penetrates lorica wall via special tube (Figs 11–14) 11
External stalk does not penetrate lorica wall via special tube (Figs 11–14) 12

11 Lorica with annular ridge(s); two zooids per lorica .... ***C. monoannulata***
Lorica without annular ridge(s); one zooid per lorica .... ***C. oviformis***

12 Diameter of aperture > maximum lorica width 13
Diameter of aperture ⩽ maximum lorica width 15

13 Lorica with two zooids 14
Lorica with one zooid .... ***C. spissa***

14 Forms pseudocolonies with several loricas attached in a chain; zooids extend just beyond aperture .... ***C. bavarica***
Not forming pseudocolonies; zooids extend up to half their length beyond aperture .... ***C. patula***

15 Lorica with distinct annular ridges or furrows 16
Lorica without annular ridges or furrows 17

16 Lorica cylindrical with evenly spaced furrows down entire length .... ***C. lapponum***
Lorica rotund with three distinct centrally located ridges .... ***C. pupa***

17 Lorica with one zooid 18
Lorica with two zooids .... ***C. kahli***

18 Macronucleus long and vermiform 19
Macronucleus short, compact and slightly curved or C-shaped 22

19 Diameter of aperture ⩾ greatest lorica width 20
Diameter of aperture < greatest lorica width .... ***C. floscularia***

20 Macronucleus straight 21
Macronucleus serpentine .... ***C. soldida***

21 Lorica 75 μm long × 40 μm wide; zooid extends up to one sixth of its length beyond aperture .... ***C. macrodisca***
Lorica 125 μm long × 75 μm wide; zooid extends up to one third of its length beyond aperture .... ***C. ovata***

22 Diameter of aperture < greatest lorica width 23
Diameter of aperture ⩾ greatest lorica width 24

23 Lorica curved; typically forms pseudocolonies with several loricas attached in a chain .... ***C. variabilis***
Lorica not curved; does not form pseudocolonies .... ***C. vaga***

24 Peristomial lip thick and prominent; external stalk without transverse folds or striae .... ***C. brevistyla***
Peristomial lip not prominently thickened; external stalk with transverse striae .... ***C. astaci***

25 Marine or brackish 26
Freshwater 73

26 Mesostyle present 27
Mesostyle absent 59

27 Endostyle present 28
Endostyle absent 52

28 Lorica with two zooids 29
Lorica with one zooid 34

29 Aperture border without clefts 30
Aperture border with one or more clefts 33

30 Lorica without annular ridges 31
Lorica with annular ridges .... ***C. rhabdota***

31 Lorica < 125 μm long; macronucleus straight 32
Lorica ≥ 125 μm long; macronucleus coiled irregularly .... ***C. trophoniae***

32 Zooids extend at least one third of their length beyond aperture; external stalk and mesostyle with conspicuous longitudinal striae .... ***C. apseudophila***
Zooids extend up to one quarter of their length beyond aperture; stalk and mesostyle with inconspicuous striae .... ***C. aplatita***

33 Aperture border with two clefts; longitudinal striae absent from mesostyle but present on endostyle .... ***C. felinska***
Aperture border with one cleft; longitudinal striae present on mesostyle but absent from endostyle .... ***C. cyathiforme***

34 Zooid extends as far as or just beyond aperture 35
Zooid extends at least one sixth of its length beyond aperture 43

35 Macronucleus curved or twisted 36
Macronucleus straight 37

36 Lorica 110–150 μm long; aperture border with clefts .... ***C. auriculata***
Lorica 70 μm long; aperture border without clefts .... ***C. cytherideae***

37 External stalk with conspicuous longitudinal striae 38
External stalk with inconspicuous longitudinal striae 41

38 Mesostyle and endostyle with conspicuous longitudinal striae 39
Mesostyle and endostyle with inconspicuous longitudinal striae .... ***C. parvula***

39 Lorica and external stalk not curved; aperture ovoid when viewed from above 40
Lorica and external stalk curved; aperture triangular when viewed from above .... ***C. triangula***

40 Lorica 70 μm long; CV situated just below peristome .... ***C. halacaricola***
Lorica 93–97 μm long; CV situated near proximal end of macronucleus .... ***C. nitocrae***

41 Diameter of aperture < maximum lorica width; lorica walls with irregular ridges and furrows 42
Diameter of aperture > maximum lorica width; lorica without ridges or furrows .... ***C. complanata***

42 Lorica 150 μm long; CV lies in centre of zooid .... ***C. elongata***
Lorica 50–62 μm long; CV lies just below peristome . ***C. parvula***

43 Pellicular striations conspicuous 44
Pellicular striations inconspicuous 47

44 Macronucleus straight 45
Macronucleus serpentine 46

45 Zooid extends up to one third of its length beyond aperture; lorica without ridges and furrows .... ***C. ceramicola***
Zooid extends up to one quarter of its length beyond aperture; lorica with ridges and furrows .... ***C. coarctata***

46 Brackish; lorica 95 μm long .... ***C. obliqua***
Marine; lorica 50–60 μm long .... ***C. simplex***

47 Zooid extends ≥ one third of its length beyond aperture 48
Zooid extends < one third of its length beyond aperture 50

48 Lorica with ridges and furrows 49
Lorica without ridges and furrows .... ***C. stylarioides***

49 Lorica 121 μm long; length of external stalk one quarter lorica length .... ***C. cyclopis***
Lorica 50–60 μm long; external stalk < one quarter lorica length .... ***C. cypridicola***

50 External stalk with inconspicuous longitudinal striae 51
External stalk with conspicuous longitudinal striae .... ***C. harpactici***

51 Lorica 120 μm long; external stalk ≥ one quarter lorica length .... ***C. cordylophora***
Lorica 60–70 μm long; external stalk < one quarter lorica length .... ***C. collaris***

52 Lorica with two zooids 53
Lorica with one zooid 54

53 Lorica curved; macronucleus short and C-shaped .... ***C. limnoriae***
Lorica not curved; macronucleus vermiform and coiled irregularly .... ***C. trophoniae***

54 External stalk with conspicuous longitudinal striae 55
External stalk with inconspicuous longitudinal striae 57

55 Macronucleus straight 56
Macronucleus serpentine .... ***C. butschlii***

56 Lorica 81 μm long; pellicular striations inconspicuous .... ***C. peloscolicis***
Lorica 53–55 μm long; pellicle clearly striated .... ***C. gammari***

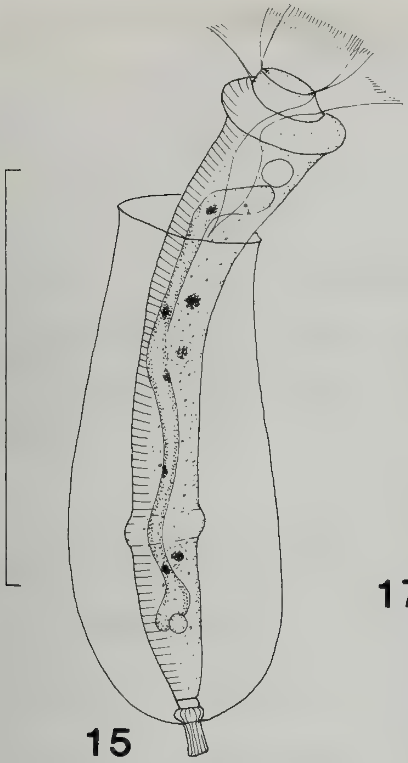
57 Aperture border without clefts 58
Aperture border with cleft .... ***C. incisa***

58 Lorica 60 μm long; zooid with annular ridge(s) .... ***C. fibripes***
Lorica 125 μm long; zooid without annular ridge(s) . ***C. arcuata***

59 Brackish 60
Marine 63

60 Diameter of aperture < maximum lorica width 61

Figs 15–17 *Cothurnia imberbis*; figs 15 & 16 after Bacon, 1965, bar = 50 μm; fig. 17 after Ehrenberg, 1831.
Figs 18 & 19 *Cothurnia acuta*; fig. 18 after Precht, 1935, bar = 50 μm; fig. 19 after Levander 1915.
Fig. 20 *Cothurnia amoyensis*, after Wang, 1935, bar = 25 μm.
Fig. 21 *Cothurnia amphicteis*, after Lang, 1948, bar = 50 μm.
Fig. 22 *Cothurnia angusta*, after Kahl, 1935, bar = 50 μm.
Fig. 23 *Cothurnia annulata*, after Sommer, 1951, bar = 50 μm.
Figs 24–26 *Cothurnia anomala*, after Stiller, 1951; fig. 24 bar = 25 μm; figs 25 & 26 variations in lorica shape.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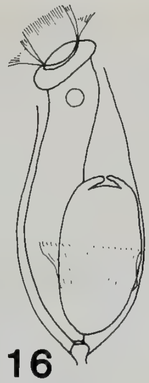
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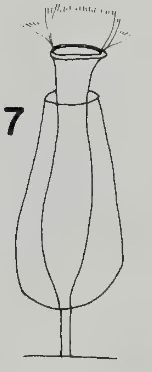
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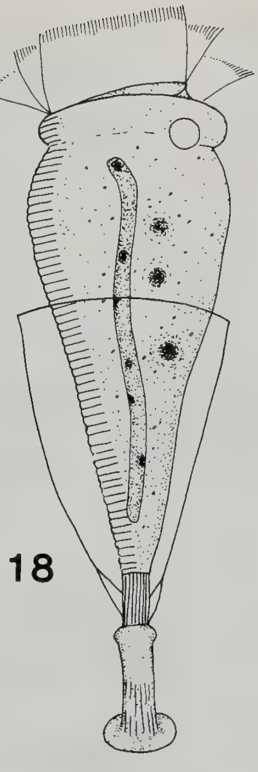
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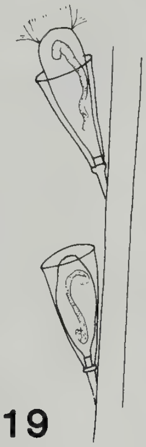
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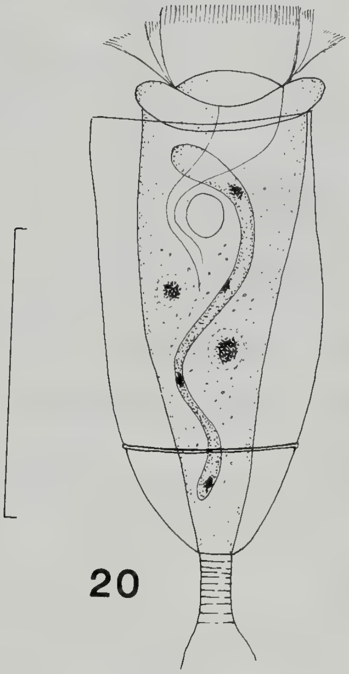
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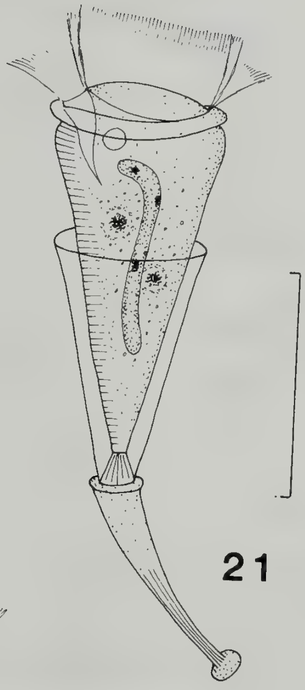
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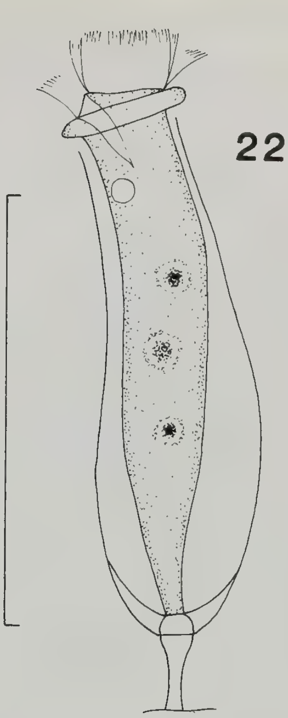
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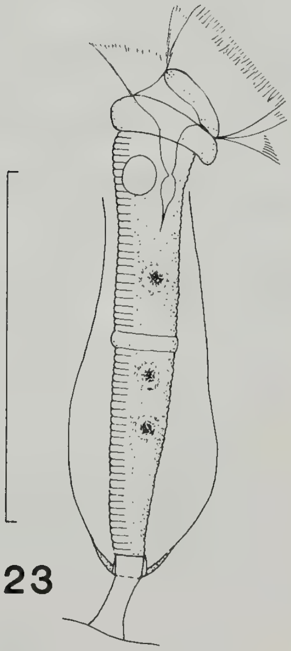
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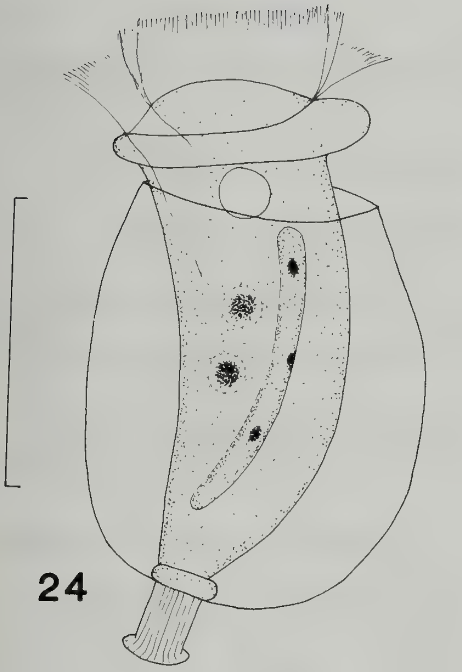
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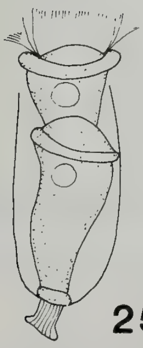
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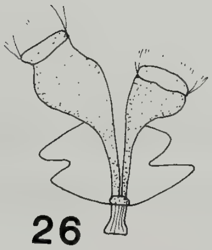
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Diameter of aperture ≥ maximum lorica width 62

61 Lorica curved, 100 μm long × 50 μm wide .... ***C. recurvata***
Lorica not curved, 60 μm long × 30 μm wide .... ***C. inflata***

62 Lorica cylindrical, 110 μm long .... ***C. fecunda***
Lorica conical, 50–56 μm long .... ***C. acuta***

63 Lorica with two zooids 64
Lorica with one zooid 66

64 Aperture border with clefts 65
Aperture border without clefts .... ***C. nodosa***

65 Lorica 90–100 μm long; zooid 150 μm long and extends up to one third of its length beyond aperture ...... ***C. sinuosa***
Lorica 70–80 μm long; zooid 85–90 μm long and extends up to one fifth of its length beyond aperture .... ***C. entzi***

66 Pellicular striations conspicuous 67
Pellicular striations inconspicuous 70

67 Lorica without ridges or furrows; zooid extends > one quarter of its length beyond aperture 68
Lorica with ridges and furrows; zooid reaches just beyond aperture .... ***C. recurvata***

68 Diameter of aperture ≤ maximum lorica width 69
Diameter of aperture > maximum lorica width ... ***C. amphicteis***

69 Lorica 40–45 μm long; peristomial lip prominently thickened .... ***C. membranoloricata***
Lorica 35 μm long; peristomial lip not prominently thickened .... ***C. maritima***

70 Lorica without annular ridges or furrows 71
Lorica with annular ridges and furrows .... ***C. cohni***

71 Aperture border without clefts 72
Aperture border with clefts .... ***C. compressa***

72 Lorica 100 μm long; length of external stalk ≥ lorica .... ***C. longipes***
Lorica 65–72 μm long; length of external stalk < lorica .... ***C. subtilis***

73 Mesostyle present 74
Mesostyle absent 83

74 Endostyle present 75
Endostyle absent 78

75 External stalk with transverse ridges or folds 76
External stalk without transverse ridges or folds 77

76 Lorica 80–100 μm; macronucleus ovoid .... ***C. plectostlya***
Lorica 60 μm; macronucleus short and curved .... ***C. propinqua***

77 Lorica cylindrical; diameter of aperture = maximum lorica width .... ***C. tekirghiolica***
Lorica rounded posteriorly; diameter of lorica < maximum lorica width .... ***C. imberbis***

78 Lorica with two zooids 79
Lorica with one zooid 80

79 Lorica 113–132 μm long; aperture border extended to form two horn-like processes .... ***C. sieboldii***
Lorica 61 μm long; aperture border without horn-like processes .... ***C. cylindrica***

80 Zooid extends > one third of its length beyond aperture 81
Zooid only reaches as far as or just beyond aperture 82

81 Macronucleus long and vermiform .... ***C. ruthae***
Macronucleus short and thick .... ***C. richtersi***

82 Zooid with prominent annular ridge(s); pellicular striations conspicuous .... ***C. elegans***
Zooid without annular ridge(s); pellicular striations inconspicuous .... ***C. angusta***

83 Lorica with two zooids 84
Lorica with one zooid 86

84 Diameter of aperture ≤ maximum lorica width 85
Diameter of aperture > maximum lorica width .... ***C. clausiens***

85 Lorica 30–40 μm long; zooid only reaches as far as or just beyond aperture .... ***C. anomala***
Lorica 71–82 μm long; zooid extends up to one third of its length beyond aperture .... ***C. oblonga***

86 External stalk does not penetrate lorica wall via special tube 88
External stalk penetrates lorica wall via special tube (Figs 11–14) 87

87 Zooid with annular ridge(s); pellicular striations conspicuous .... ***C. annulata***
Zooid without annular ridge(s); pellicular striations inconspicuous .... ***C. asymmetrica***

88 External stalk with transverse folds and ridges 89
External stalk without transverse folds and ridges 91

89 Diameter of aperture = maximum lorica width 90
Diameter of aperture < maximum lorica width .... ***C. curva***

90 Macronucleus short and slightly curved; pellicular striations inconspicuous .... ***C. canthocampti***
Macronucleus C-shaped; pellicular striations inconspicuous .... ***C. lata***

91 Zooid reaches as far as or just beyond aperture 92
Zooid extends > one quarter of its length beyond aperture 94

92 Lorica 48–55 μm long; external stalk with inconspicuous longitudinal striae 93
Lorica 70–72 μm long; external stalk with conspicuous longitudinal striae .... ***C. carinogammari***

93 External stalk 10–15 μm long; zooid with posterior annular ridge(s) .... ***C. irregularis***
External stalk 2 μm long; zooid without annular ridge(s) .... ***C. asimmetrica***

94 Lorica 125 μm long 95

Figs 27 & 28 *Cothurnia antarctica*, after Daday, 1911, bar = 50 μm.

Figs 29 & 30 *Cothurnia aplatita*; fig. 29 after Felinska, 1965 (called *Cothurnia aplatita* var. *flexa*); fig. 30 after Stiller, 1939, bar = 50 μm.

Fig. 31 *Cothurnia apseudophila*, after Lang, 1948, bar = 100 μm.

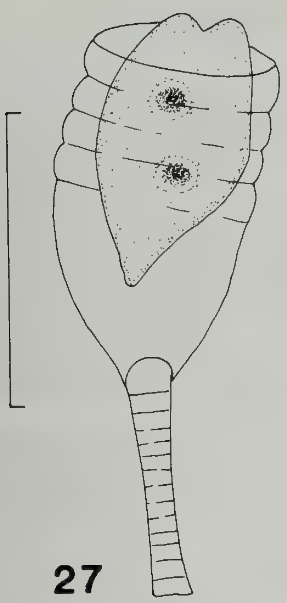
Figs 32–34 *Cothurnia arcuata*; figs 32 & 33 after Mereschkowsky, 1879, bar = 100 μm; fig. 34 after Gourret and Roeser, 1886 (called *Cothurnia fusiformis*).

Figs 35 & 36 *Cothurnia asimmetrica*, after Banina and Polyakova, 1977, bar = 25 μm.

Figs 37 & 38 *Cothurnia astaci* after Matthes and Guhl, 1973; fig. 37 bar = 50 μm; fig. 38 showing variation in lorica and external talk.

Figs 39 & 40 *Cothurnia asymmetrica*, after Sommer, 1951.

Figs 41–43 *Cothurnia auriculata*; figs 41 & 42 after Stiller, 1939; fig. 43 after Felinska, 1965, bar = 100 μm.



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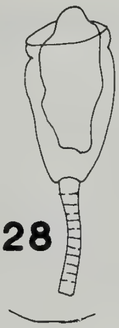

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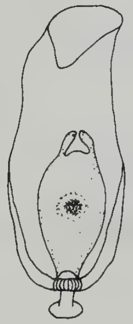

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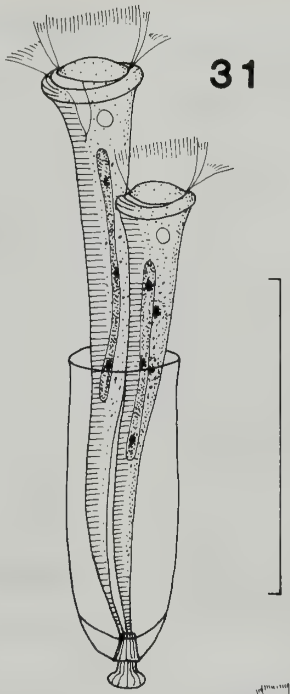

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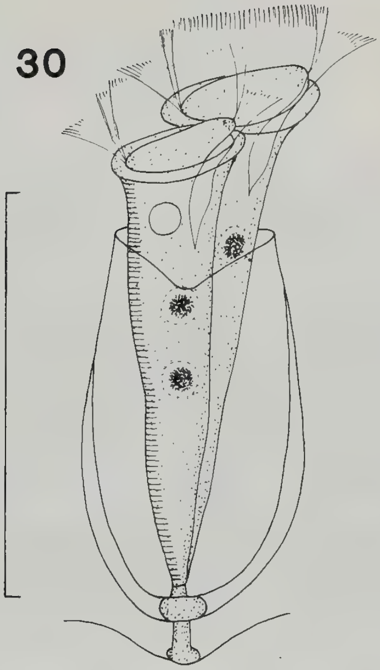

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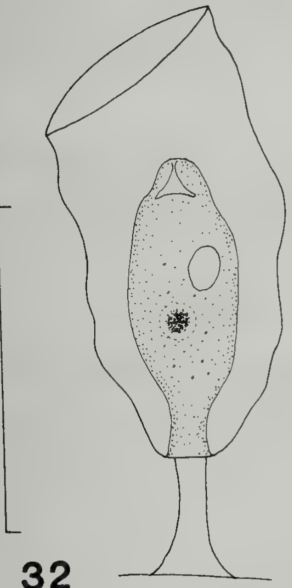

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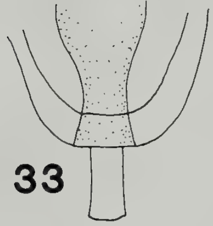

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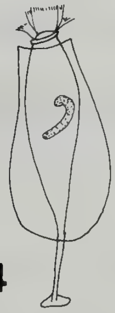

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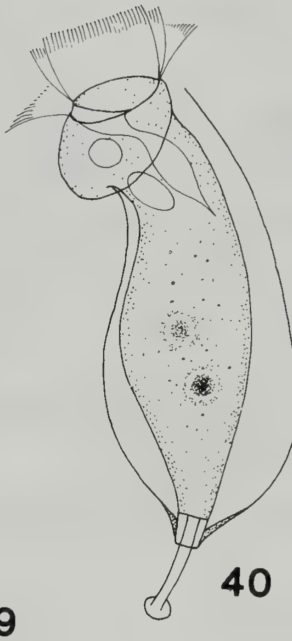

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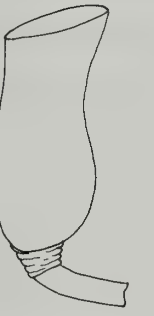

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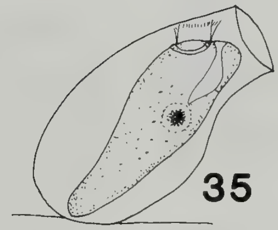

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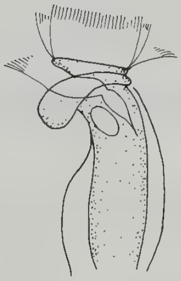

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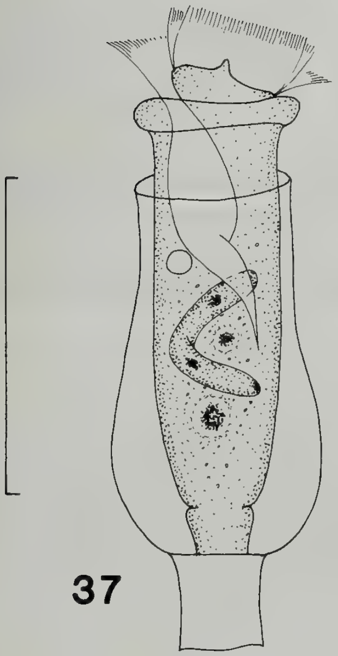

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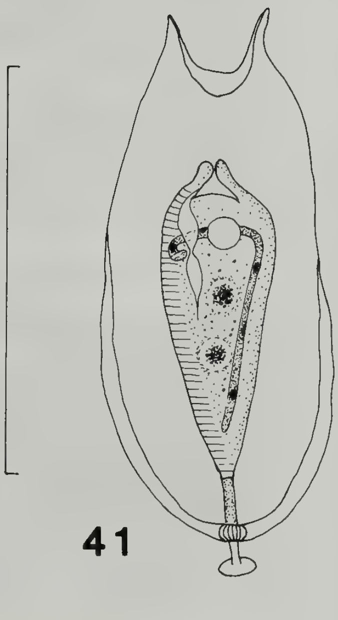

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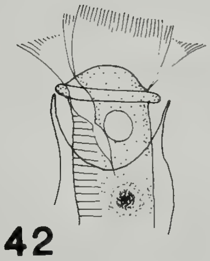

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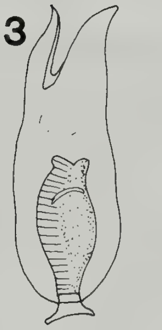

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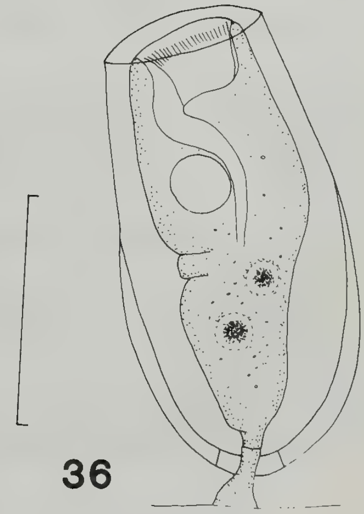

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Lorica 35–40 μm long .... *C. minutissima*

95 Lorica 200 μm long; pellicular striations conspicuous .... *C. irregularis*

Lorica 127 μm long; pellicular striations inconspicuous .... *C. plachteri*

Species descriptions

Cothurnia imberbis Ehrenberg, 1831

Sincothurnia imberbis (Ehrenberg, 1831) Jankowski, 1985

DESCRIPTION (Figs 15–17). Lorica 45–85 μm long × 20–40 μm wide. Aperture 10–20 μm in diameter. External stalk 15 μm long, mesostyle short and broad, endostyle short and inconspicuous. External stalk and mesostyle with conspicuous longitudinal striae. Zooid 57–95 μm long × 8–18 μm wide, extending about one fifth of its length beyond aperture. Annular ridge in region of telotroch band. Peristomial lip well developed, 13–18 μm in diameter. CV situated just below peristome. Macronucleus straight, curved anteriorly and lies longitudinally in zooid. Pellicle with fine striations.

HABITAT. Freshwater, attached to a variety of plant and animal substrates.

NOTE. This, the type species of the genus, was redescribed by Bacon (1968).

Cothurnia acuta Levander, 1915

Semicothurnia acuta (Levander, 1915) Jankowski, 1976

DESCRIPTION (Figs 18 & 19). Lorica conical, 50–56 μm long × 30 μm wide. Aperture 31 μm in diameter. External stalk broad, up to 8 μm long; endostyle also broad, up to 4 μm long; mesostyle absent. Zooid 60 μm long × 20 μm wide and extends up to one third of its length beyond aperture. Peristomial lip 18 μm in diameter. Macronucleus lies longitudinally in zooid, vermiform and curved anteriorly. Pellicular striations conspicuous.

HABITAT. Brackish water, originally isolated as an epizoite of the polychaetes *Harmothoe sarsi* and *H. imbricata* (Levander, 1915).

NOTE. Jankowski (1976) erected the genus *Semicothurnia* for *C. acuta* on the basis of its broad external stalk. The stalk is not sufficiently distinctive to separate a new genus so this species is retained in the genus *Cothurnia*.

Cothurnia amoyensis Wang, 1935

DESCRIPTION (Fig. 20). Lorica 35–40 μm long × 18–20 μm wide with annular ridge near posterior end; lorica cylindrical above the ridge and conical below. External stalk 6 μm long with transverse annulations. Mesostyle and endostyle absent. Zooid extends just beyond aperture, 45 μm long × 15 μm wide. Peristomial lip well developed, 18 μm in diameter. Disc convex. CV situated one quarter of way down zooid. Macronucleus vermiform, curved at both ends and extends almost entire length of zooid. Pellicular striations inconspicuous.

HABITAT. Marine, originally found in a laboratory culture containing decomposing algae (Wang, 1935).

Cothurnia amphicteis Lang, 1948

Semicothurnia amphicteis (Lang, 1948) Jankowski, 1985

DESCRIPTION (Fig. 21). Lorica conical, 53–56 μm long × 35 μm wide. Aperture 35–37 μm in diameter. External stalk 54–57 μm long, lower half with conspicuous longitudinal striae, upper half granular, and with ring-like thickening at point of attachment to lorica. Endostyle short, broad and with conspicuous longitudinal striae. Mesostyle absent. Zooid conical, 85 μm long × 40 μm wide, and extends between one third and one half of its length beyond aperture. Peristomial lip well developed, 45 μm in diameter. Disc convex. CV lies just below peristome. Macronucleus elongate, slightly curved anteriorly. Pellicular striations conspicuous.

HABITAT. Marine, originally found attached to the setae of *Amphicteis gunneri* in coastal waters of Sweden (Lang, 1948).

Cothurnia angusta Kahl, 1933

DESCRIPTION (Fig. 22). Lorica elongate, 60 μm long × 15–23 μm wide, rounded posteriorly. Aperture 10 μm in diameter. External stalk about 10 μm long, mesostyle short, endostyle absent. Zooid 70 μm long × 12 μm wide and extends just beyond aperture. Peristome 18 μm diameter. CV situated about one sixth of way down zooid. Pellicular striations inconspicuous.

HABITAT. Brackish or freshwater, originally found attached to cyprid ostracods (Kahl, 1933; Precht, 1935); also found on *Enteromorpha intestinalis* (Sommer, 1951).

Cothurnia annulata Stokes, 1885

Cothurniopsis annulata (Stokes, 1885) Penard, 1922

DESCRIPTION (Fig. 23). Lorica 55 μm long × 25 μm wide and rounded posteriorly. External stalk short; endostyle short and with conspicuous longitudinal striae; mesostyle absent. Zooid slender, 65 μm long × 12 μm wide and with centrally located annular ridge. Peristomial lip 15 μm in diameter. CV situated about one sixth of way down zooid. Macronucleus straight and lies longitudinally in centre of zooid. Pellicular striations conspicuous.

HABITAT. Freshwater, originally isolated from North American ponds attached to *Myriophyllum* (Stokes, 1885, 1888); also found on the aquatic plants and algae *Lemna*, *Hydroictyon reticulatum* and *Enteromorpha intestinalis* (Sommer, 1951).

NOTE. Although the name *C. annulata* was originally mentioned by Stokes in 1885, a detailed description and diagram did not appear until three years later (Stokes, 1888). *C. annulata* was redescribed by Penard (1922) and by Sommer (1951).

Cothurnia anomala Stiller, 1951

DESCRIPTION (Figs 24–26). Lorica 30–40 μm long × 15–25 μm wide. Diameter of aperture equal to maximum lorica width. External stalk broad, 5 μm long; endostyle short and inconspicuous; mesostyle absent. Two zooids per lorica, one not reaching as far as aperture, the other extending just beyond aperture. Peristomial lip well developed, 20 μm in diameter. CV situated just below peristome. Macronucleus slightly curved and lies longitudinally in zooid. Pellicular striations inconspicuous.

HABITAT. Freshwater, originally isolated from Lake Balaton as an epizoite of the amphipod *Corophium curvispinum* (Stiller, 1951).

NOTE. If coloniality (*sensu* Jankowski, 1985) is accepted as a generic character among cothurnids, this species should be included in the genus *Sincothurnia*.

Cothurnia antarctica (Daday, 1911) n. comb.

Cothurniopsis antarctica Daday, 1911

DESCRIPTION (Figs 27 & 28). Lorica 50–60 μm long × 30 μm wide with 1–4 annular constrictions on anterior half. Aperture 30 μm in diameter. External stalk 40–50 μm long and with transverse folds. Endostyle and mesostyle not observed. Zooid extends just beyond aperture. Macronucleus compact. Pellicular striations inconspicuous.

HABITAT. Marine, originally found in the Antarctic region as an epizoite of the ostracod *Philomedes laevipes* (Daday, 1911).

Cothurnia aplatita Stiller, 1939

Cothurnia aplatita var. *flexa* Felinska, 1965

DESCRIPTION (Figs 29 & 30). Lorica 45–65 μm long × 25–30 μm wide and typically covered with particles of sand and detritus. External stalk and endostyle short; mesostyle short, broad and with conspicuous longitudinal striae. Two zooids per lorica, each 70–80 μm long × 20–25 μm wide and extending up to one quarter of its length beyond aperture. Peristomial lip 25 μm in diameter. CV situated just below peristome. Macronucleus elongate. Pellicle with fine striations.

HABITAT. Marine, originally isolated from laboratory aquaria at Helgoland attached to Campanulariaceae (Stiller, 1939); also found in marine aquaria at Plymouth attached to green algae (Felinska, 1965).

NOTE. According to Felinska (1965) *C. aplatita* and *C. aplatita* var. *flexa* are identical apart from minor differences in the shape of the lorica. These differences are considered to be insufficient for the recognition of the two organisms as separate taxa. Furthermore, if coloniality (*sensu* Jankowski, 1985) is accepted as a generic character among cothurnids, this species should be included in the genus *Sincothurnia*.

Cothurnia apseudophila Lang, 1948

Sincothurnia apseudophila (Lang, 1948) Jankowski, 1985

DESCRIPTION (Fig. 31). Lorica cylindrical, 88–92 μm long × 29–31 μm wide, and rounded posteriorly. Aperture 29–31 μm in diameter. External stalk and mesostyle 7–8 μm long with conspicuous longitudinal striae; endostyle 1.5 μm long. Two zooids per loria one of which is always larger than the other; larger zooid 164 μm long × 20 μm wide, extending up to one half of its length beyond aperture; smaller zooid 128 μm long × 17 μm wide, extending up to one third of its length beyond aperture. Peristome 25–30 μm in diameter. CV situated just below peristome. Macronucleus straight and lies longitudinally in zooid. Pellicular striations conspicuous.

HABITAT. Marine, originally found on the setae of *Apseudes spinosus* in Swedish coastal waters (Lang, 1948).

Cothurnia arcuata Mereschkowsky, 1879

Cothurnia arenata (Mereschkowsky, 1879) Zelinka, 1928
Cothurnia fusiformis (Gourret & Roeser, 1886) Zelinka, 1928

DESCRIPTION (Figs 32–34). Lorica 125 μm long × 60–65 μm wide, cylindrical and curved. External stalk up to 40 μm long, broad and with large basal disc. Mesostyle short and broad. Endostyle absent. Zooid 125 μm long × 35 μm wide and just reaches aperture. Peristomial lip 25 μm in diameter. CV situated near centre of zooid. Macronucleus C-shaped and lies in centre of zooid. Pellicular striations inconspicuous.

HABITAT. Marine, originally isolated from the White Sea (Mereschkowsky, 1879); also isolated from the Port of Marseille (Gourret & Roeser, 1886).

Cothurnia asimmetrica Banina and Polyakova, 1977

DESCRIPTION (Figs 35 & 36). Lorica 48–52 μm long × 25 μm wide and typically inclined at an angle to substrate. Aperture 12–18 μm in diameter. External stalk 2 μm long and penetrates lorica wall via special tube; endostyle 1 μm long; mesostyle absent. Zooid 50 μm long × 17 μm wide and just reaches aperture. CV situated one third of way down zooid. Pellicular striations inconspicuous.

HABITAT. Freshwater, originally found on *Cladophora* (Banina and Polyakova, 1977).

Cothurnia astaci Stein, 1854

Cothurniopsis astaci (Stein, 1854) Entz, 1884

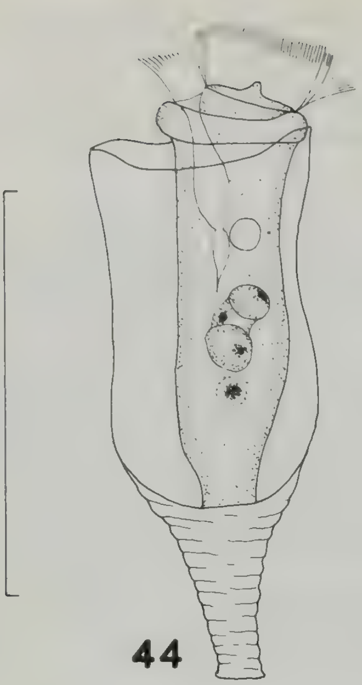
DESCRIPTION (Figs 37 & 38). Lorica 65–90 μm long × 35–45 μm wide and rounded posteriorly. Aperture 40 μm in diameter. External stalk 15 μm long, slightly curved and with transverse folds. Mesostyle and endostyle absent. Zooid slender, 75 μm long × 20 μm wide and extends just beyond aperture. CV lies one third of way down zooid. Macronucleus short, C-shaped and situated in centre of zooid. Pellicular striations inconspicuous.

HABITAT. Freshwater, found on a variety of substrates including the crayfish *Astacus fluviatilis* and *A. leptodactylus* (Matthes and Guhl, 1973), and on *Entomostraca* (Kahl, 1935).

NOTE. A recent redescription of this species was given by Matthes and Guhl (1973).

Cothurnia asymmetrica Sommer, 1951

DESCRIPTION (Figs 39 & 40). Lorica 50 μm long × 25 μm wide and with prominent bulge about two thirds of way down. Aperture 12 μm in diameter. Neck region below aperture curved. External stalk slender, about 10 μm long; endostyle short; mesostyle absent. Zooid 50 μm long × 15 μm wide and extends just beyond aperture. Peristomial lip 18 μm in diameter and prominently thickened. CV large, ovoid and lies below peristome. Pellicular striations inconspicuous.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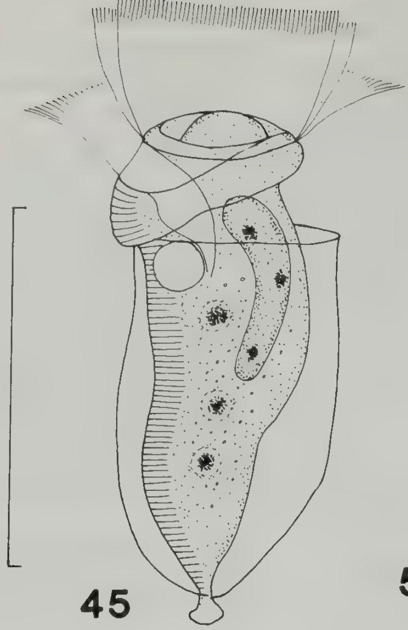
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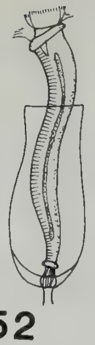
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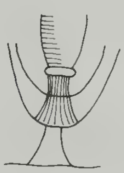
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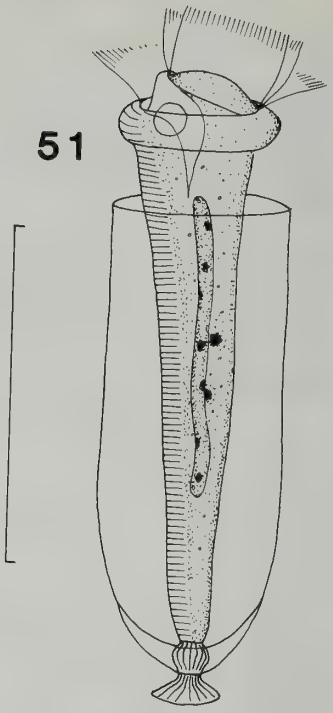
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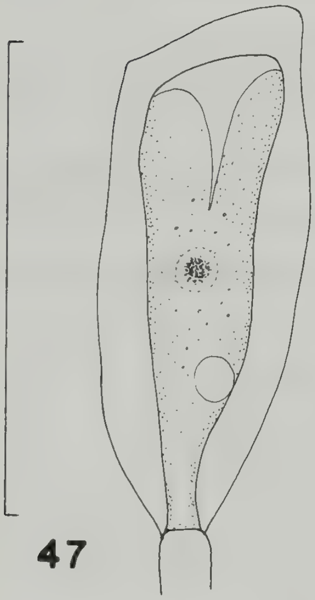
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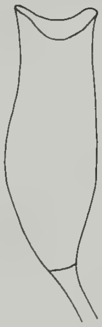
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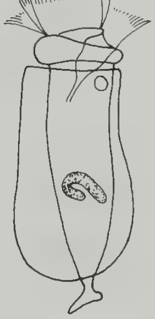
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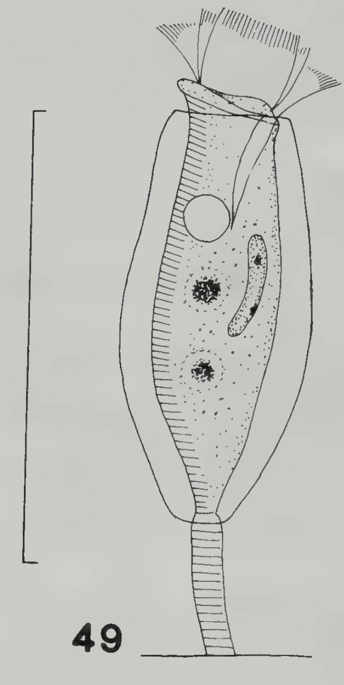
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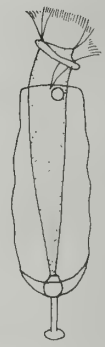
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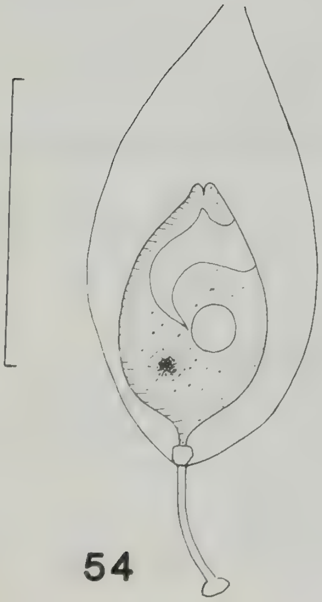
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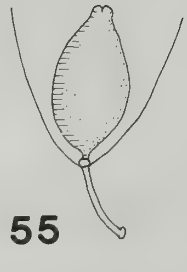
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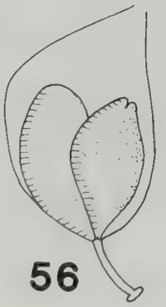
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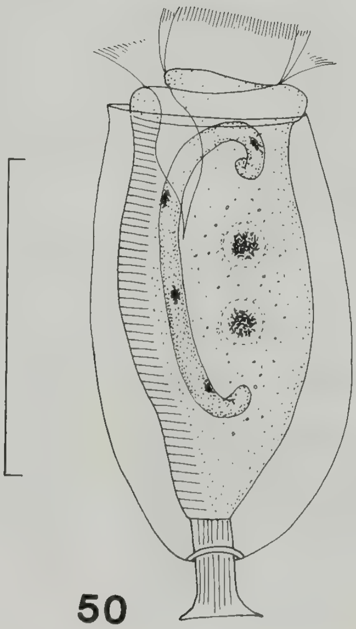
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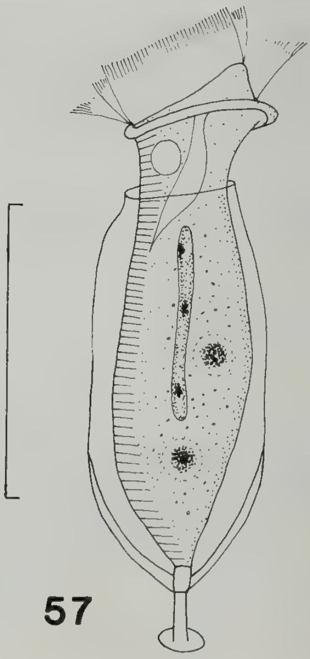
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HABITAT. Freshwater, originally found attached to *Cladophora* and *Enteromorpha intestinalis* (Sommer, 1951).

Cothurnia auriculata Stiller, 1939

Cothurnia auriculata var. *flexa* Felinska, 1965
Sincothurnia auriculata (Stiller, 1939) Jankowski, 1985
Sincothurnia flexa (Felinska, 1965) Jankowski, 1985

DESCRIPTION (Fig. 41–43). Lorica irregular, 110–150 μm long × 45–60 μm wide. Aperture narrow with two clefts in aperture border. External stalk short and with broad basal disc; mesostyle short, broad and with conspicuous longitudinal striae; endostyle slender and variable in length. Zooid cylindrical in shape, 20 μm wide and just reaches aperture. Peristomial lip 25 μm in diameter. Disc convex. CV lies just below peristome. Macronucleus vermiform with anterior end curved horizontally across peristome. Pellicle with fine striations.

HABITAT. Marine, originally isolated from the North Sea attached to *Cladophora* (Stiller, 1939); also reported from marine aquaria at Plymouth (Felinska, 1965).

Cothurnia bavarica Matthes and Guhl, 1973

DESCRIPTION (Fig. 44). Lorica 85–93 μm long × 49–59 μm wide. Aperture 60 μm in diameter. External stalk 33–35 μm long × 10–12 μm wide and with transverse folds. Mesostyle and endostyle absent. Forms pseudocolonies with loricas of several individuals attached to each other via external stalks to form a chain. Two zooids per lorica, each 87–118 μm long × 20–35 μm wide and extends just beyond aperture. Peristomial lip well developed, 35 μm in diameter. Disc raised and umbilicate. CV situated near mid-region of infundibulum which reaches centre of body. Macronucleus thick, horseshoe-shaped and lies in centre of zooid. Pellicular striations inconspicuous.

HABITAT. Freshwater, originally found attached to the crayfish *Astacus leptodactylus* and *Cambarus affinis* (Matthes and Guhl, 1973).

NOTE. If coloniality (*sensu* Jankowski, 1985) is accepted as a generic character, this species should be included in the genus *Sincothurnia*.

Cothurnia brevistyla Nenninger, 1948

DESCRIPTION (Figs 45 & 46). Lorica cylindrical 43.5–54.9 μm long × 20–25 μm wide, and rounded posteriorly. External stalk short and with broad basal disc. Endostyle and mesostyle absent. Zooid 58 μm long × 20 μm wide. Peristomial lip well developed, 25 μm in diameter. Disc convex. CV lies just below peristome. Macronucleus thick, slightly curved and lies longitudinally in zooid. Pellicle with fine striations.

HABITAT. Freshwater, originally found attached to algae from canal water in Germany (Nenninger, 1948).

Cothurnia butschlii Zelinka, 1913

DESCRIPTION (Figs 47 & 48). Lorica 53.2 μm long × 27 μm wide and tapers towards stalk. Aperture 25 μm in diameter. External stalk 10 μm long × 4 μm wide; endostyle short; mesostyle absent. External stalk and endostyle with continuous longitudinal striae. Zooid 25–30 μm long when contracted. Macronucleus C-shaped and lies longitudinally in zooid. Pellicular striations inconspicuous.

HABITAT. Marine, originally found attached to echinodera (Zelinka, 1913).

NOTE. The data above is based on observations of contracted specimens only. Uncontracted specimens of *C. butschlii* have yet to be described.

Cothurnia canthocampti Stokes, 1886

Cothurniopsis canthocampti Monard, 1919

DESCRIPTION (Fig. 49). Lorica 84–95 μm × 40–42 μm wide. Aperture 25 μm in diameter. External stalk 20–30 μm long and with regular transverse folds; endostyle short and inconspicuous; mesostyle absent. Zooid 85 μm long × 30 μm wide extending just beyond aperture. CV situated one third of way down zooid. Macronucleus short, curved and lies longitudinally in centre of body. Pellicular striations conspicuous.

HABITAT. Freshwater, originally found on *Canthocamptus minutus* in North America (Stokes, 1886).

Cothurnia carinogammari Stiller, 1953

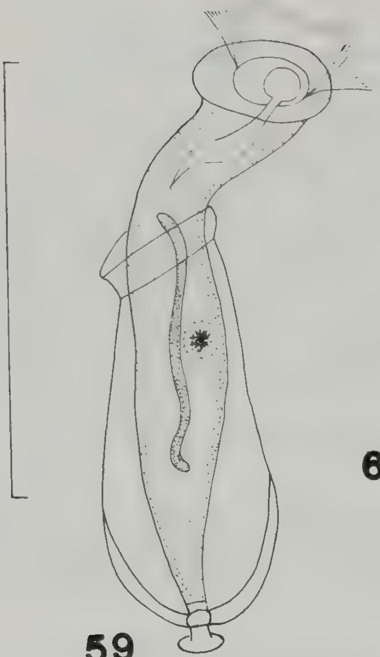
DESCRIPTION (Fig. 50). Lorica 70–72 μm × 40–42 μm wide. Aperture 25–30 μm diameter. External stalk 10 μm long; endostyle short and broad; mesostyle absent. Zooid 75 μm long × 25 μm wide and reaches just beyond aperture. Peristomial lip 25 μm in diameter. Macronucleus elongate, C-shaped and lies longitudinally in zooid. Pellicle with fine transverse striations.

HABITAT. Freshwater, originally found attached to the crustacean *Gammarus* (Stiller, 1953).

Cothurnia ceramicola Kahl, 1933

DESCRIPTION (Figs 51–53). Lorica 65–77 μm long × 30 μm wide and rounded posteriorly. Aperture 25 μm in diameter.

Fig. 44 *Cothurnia bavarica*, after Matthes and Guhl, 1973, bar = 100 μm.
Figs 45 & 46 *Cothurnia brevistyla*, after Nenninger, 1948, bar = 50 μm.
Figs 47 & 48 *Cothurnia butschlii*, after Zelinka, 1928, bar = 50 μm.
Fig. 49 *Cothurnia canthocampti*, after Stokes, 1886, bar = 100 μm.
Fig. 50 *Cothurnia carinogammari*, after Stiller, 1953, bar = 50 μm.
Figs 51–53 *Cothurnia ceramicola*; fig. 51 after Precht, 1935, bar = 50 μm; figs 52 & 53 after Kahl, 1933.
Figs 54–56 *Cothurnia clausiens*, after Stiller, 1951, bar = 25 μm.
Figs 57 & 58 *Cothurnia coarctata*; fig. 57 after Felinska, 1965, bar = 50 μm; fig. 58 after Kahl, 1935.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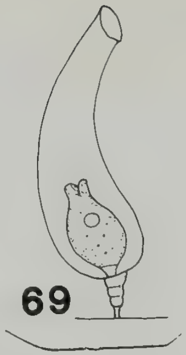
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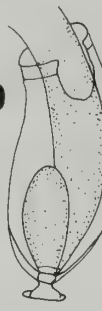
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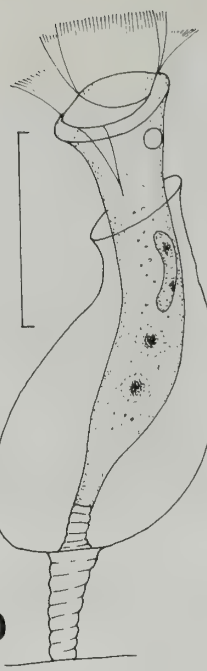
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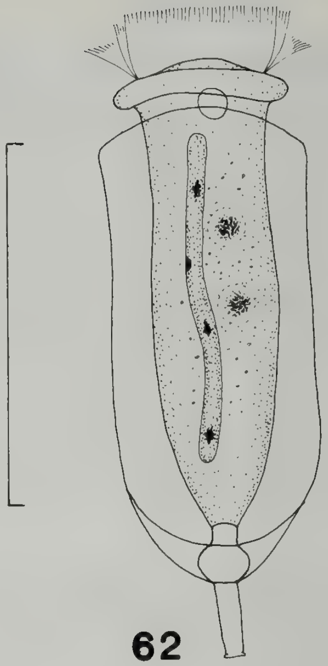
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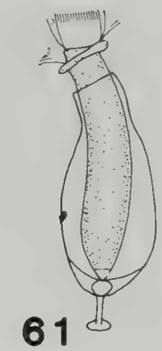
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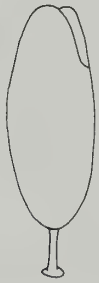
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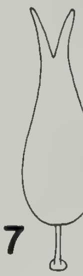
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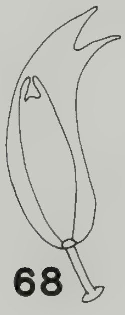
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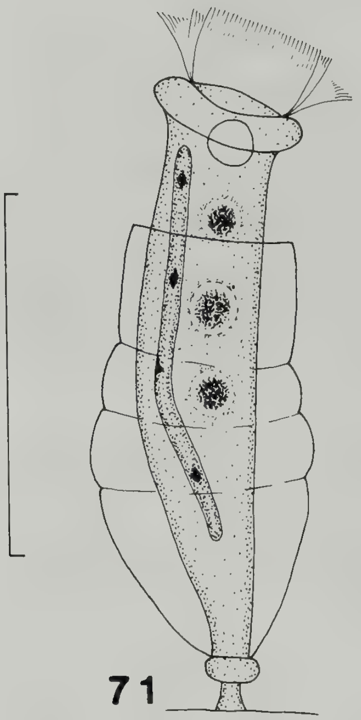
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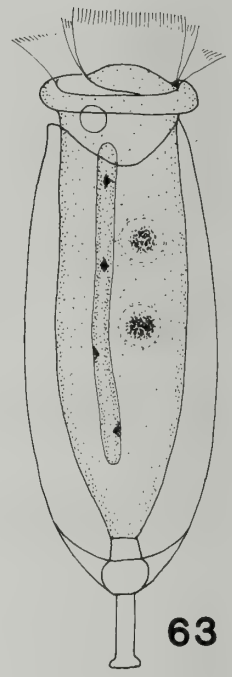
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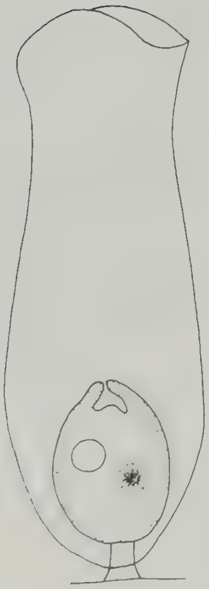
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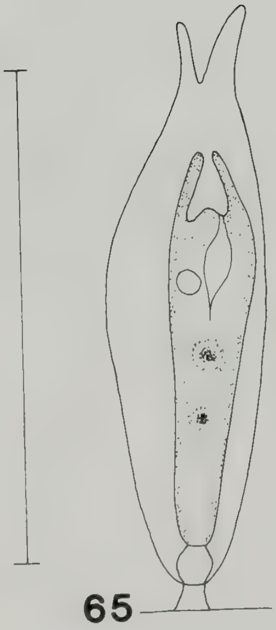
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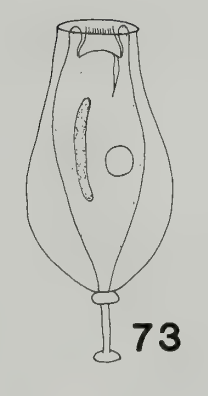
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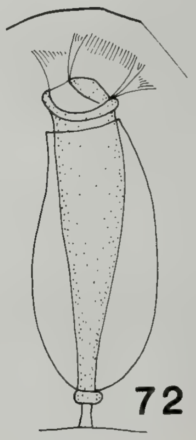
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External stalk and endostyle short; mesostyle short, broad and with conspicuous longitudinal striae. Two zooids may be present per lorica, each 80 μm long × 15 μm wide and extending up to one third of its length beyond aperture. Peristomial lip 20 μm in diameter. Disc convex. Macronucleus vermiform, extending almost entire length of zooid. Pellicular striations conspicuous.

HABITAT. Marine, originally found as an epibiont of the alga *Ceramium* (Kahl, 1933). Also found attached to the bryozoa *Crisia eburnea* and *Cribilina punctata*, the polychaete *Spirorbis spirorbis* and the cnidarian *Laomedea loveni* (Precht, 1935), and by Felinska (1965) attached to algae collected at sea and from laboratory aquaria at Plymouth.

NOTE. If coloniality (*sensu* Jankowski, 1985) is accepted as a generic character, this species should be included in the genus *Sincothurnia*.

Cothurnia clausiens Stiller, 1951

DESCRIPTION (Figs 54–56). Lorica asymmetrical, 35–50 μm long × 20–35 μm wide. External stalk about one third lorica length, slender and curved; endostyle short; mesostyle absent. Two zooids may be present per lorica, each 25–35 μm long when contracted. CV lies near centre of zooid. Macronucleus vermiform and situated longitudinally in body. Pellicle with fine striations.

HABITAT. Freshwater, originally found attached to arthropods from Lake Balaton (Stiller, 1951).

NOTE. Stiller (1951) stated that the CV is filled by a second CV nearby. This second CV is most probably a canal in which water collects before passing into the CV. Furthermore, if coloniality (*sensu* Jankowski, 1985) is accepted as a generic character, this species should be included in the genus *Sincothurnia*.

Cothurnia coarctata Kahl, 1933

DESCRIPTION (Figs 57 & 58). Lorica 66–75 μm long × 30 μm wide with transverse ridges and furrows. Aperture 20–25 μm in diameter. External stalk slender, 15–20 μm long; mesostyle and endostyle both short. Zooid 85 μm long × 25 μm wide, extending about one quarter of its length beyond aperture. Peristomial lip 30 μm in diameter. Disc flat and obliquely raised. Macronucleus straight and lies longitudinally in body. Pellicular striations conspicuous.

HABITAT. Marine, originally found attached to debris from marine aquaria at Kiel (Kahl, 1933).

NOTE. *C. coarctata* was redescribed by Felinska (1965) from specimens found on green algae at Plymouth.

Cothurnia cohni (Cohn, 1866) Kent, 1881

Cothurnia pupa Cohn, 1866

DESCRIPTION (Fig. 74). Lorica 60 μm long × 20 μm wide and pale red in colour. Upper two thirds of lorica conical, lower third rounded with several conspicuous annular ridges and furrows. External stalk broad, 15 μm long; endostyle 50 μm long and with transverse striae; mesostyle absent. Zooid 50 μm long extending just beyond aperture, slender and with an equatorial swelling. Peristomial lip well developed, 15–20 μm in diameter.

HABITAT. Marine.

NOTE. *C. pupa* Cohn, 1866 was renamed *C. cohni* by Kent (1881) in order to solve the problem of homonymy with *C. pupa* Eichwald, 1849.

Cothurnia collaris Kahl, 1933

C. collaris var. *incisa* Felinska 1965

DESCRIPTION (Figs 59–61). Lorica rotund, 60–100 μm long × 30–45 μm wide. Aperture 15 μm wide and inclined at an angle oblique to the main lorica axis. Neck short and curved. Aperture border occasionally with cleft. External stalk short and slender; mesostyle short and broad with conspicuous longitudinal striae; endostyle short. Zooid cylindrical, 70–150 μm long × 15–25 μm wide, extending up to one third of its length beyond aperture. Diameter of peristomial lip slightly greater than maximum body width. Macronucleus elongate and lies longitudinally in centre of body. Pellicular striations inconspicuous.

HABITAT. Marine or brackish, originally found attached to algae from laboratory tanks at Kiel (Kahl, 1933).

NOTE. *C. collaris* was redescribed by Stiller (1939) and Felinska (1965).

Cothurnia complanata Precht, 1935

DESCRIPTION (Figs 62 & 63). Lorica 78–81 μm long × 32–35 μm wide. External stalk slender, 12–15 μm long; mesostyle short and broad; endostyle short and inconspicuous. Zooid 80 μm long × 24 μm wide and extends just beyond aperture. Peristomial lip 30 μm in diameter. CV lies just beneath peristome. Macronucleus straight and lies longitudinally in zooid. Pellicular striations inconspicuous.

HABITAT. Marine, originally found as an epibiont of the polychaete *Stylarioides plumosus* (Precht, 1935).

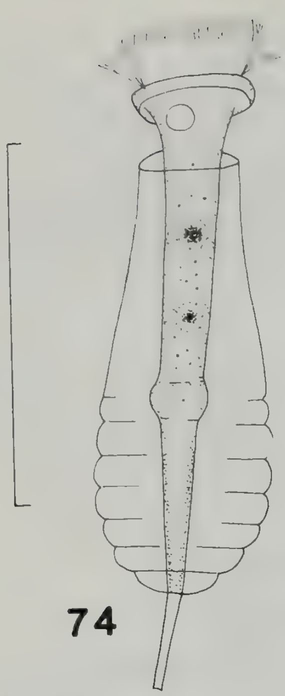
Figs 59–61 *Cothurnia collaris*, bar = 100 μm; figs 59 & 60 composite after Felinska, 1965; fig. 61 after Kahl, 1935.

Figs 62 & 63 *Cothurnia complanata*, after Precht, 1935, bar = 100 μm; fig. 62 ventral view; fig. 63 lateral view.

Figs 64–68 *Cothurnia compressa*; figs 64 & 65 after Claparede and Lachmann, 1858, bar = 100 μm; figs 66 & 67 after Kahl, 1935 (called *Cothurnia compressula*); fig. 68 after Kahl, 1935 (called *Cothurnia flexa*).

Figs 69 & 70 *Cothurnia curva*; fig. 69 composite after Kent, 1881 (called *Cothurnia gracilis*); fig. 70 after Stein, 1867, bar = 50 μm.

Figs 71–73 *Cothurnia curvula*; figs 71 & 72 after Entz, 1884, bar = 50 μm; fig. 73 after Stiller, 1971.



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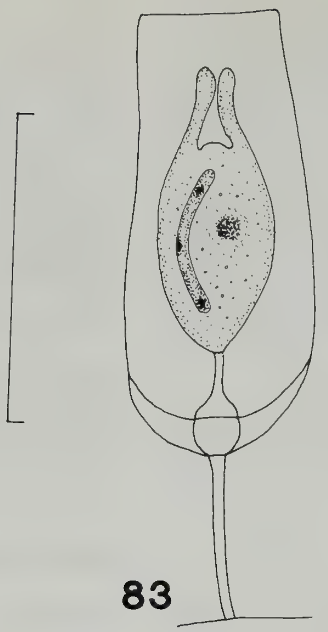

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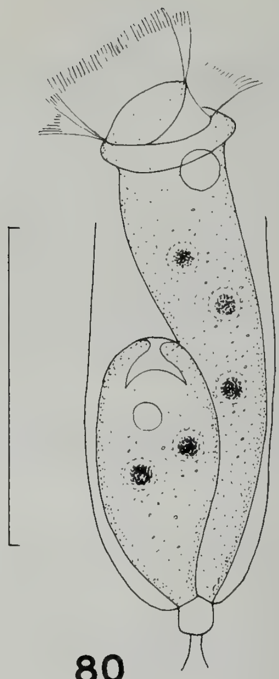

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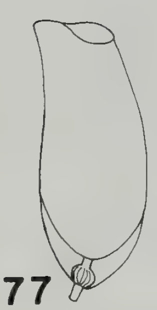

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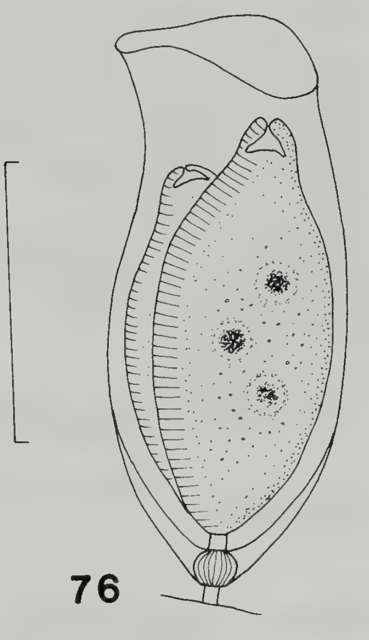

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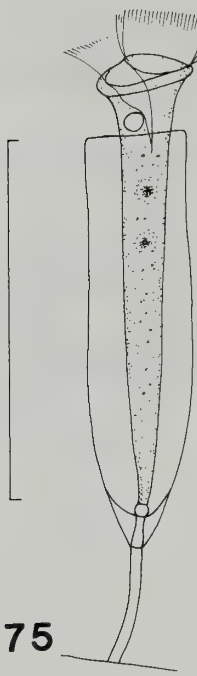

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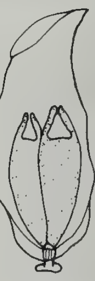

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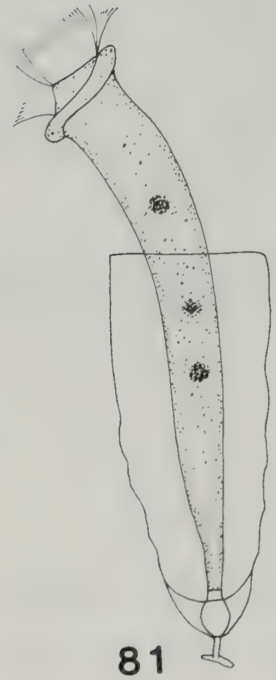

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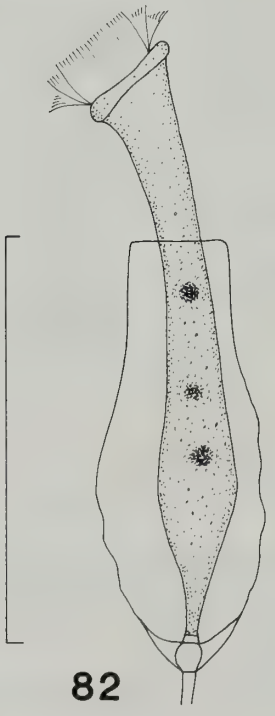

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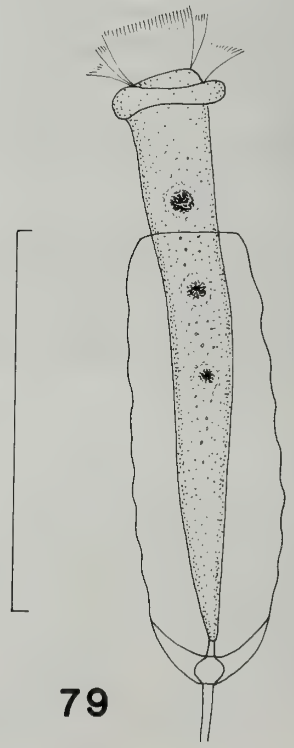

79

Cothurnia compressa Claparede and Lachmann, 1858

Cothurnia compressa var. *flexa* Wailes, 1928
Cothurnia compressula (Wailes, 1928) Kahl, 1933
Cothurnia flexa Kahl, 1935
Sincothurnia compressa (Claparede and Lachmann, 1858) Jankowski, 1985
Sincothurnia compressula (Wailes, 1928) Jankowski, 1985

DESCRIPTION (Figs 64–68). Lorica 100–140 μm long × 50 μm wide. Aperture elliptical when viewed from above, 45 μm × 15 μm. Aperture border with two deep clefts. External stalk short, endostyle short and broad, mesostyle absent. Contracted zooid 110 μm long × 30 μm wide. CV situated one quarter of way down zooid. Pellicular striations inconspicuous.

HABITAT. Marine, originally found attached to bryozoa and algae (Claparede and Lachmann, 1858).

NOTE. Stiller (1939) and Felinska (1965) described cothurnids which they identified as *C. compressa*, although both of these organisms differ from Claparede and Lachmann's (1858) *C. compressa* in that they possess a mesostyle. *C. compressa* Stiller, 1939 appears to be synonymous with *C. auriculata*, while *C. compressa* Felinska, 1965 closely resembles *C. ceramicola*.

Cothurnia cordylophorae Kahl, 1933

DESCRIPTION (Fig. 75). Lorica cylindrical, 120 μm long × 35 μm wide. Aperture 35 μm in diameter. External stalk 40 μm long; mesostyle short and broad; endostyle short and inconspicuous. Zooid elongate, 160 μm long × 15 μm wide and extends one sixth of its length beyond aperture. Pellicular striations inconspicuous.

HABITAT. Brackish water, originally found as an epizoite of the cnidarian *Cordylophora* sp. (Kahl, 1933); also found by Precht (1935) on *Cordylophora caspia*.

Cothurnia curva Stein, 1867

Cothurnia gracilis Kent, 1881.

DESCRIPTION (Figs 69 & 70). Lorica curved, 70–100 μm long × 35–40 μm wide, colourless when young becoming red when mature. Aperture 15–20 μm in diameter. Neck region just below aperture narrow and curved. External stalk broad; endostyle slender; mesostyle absent. Endostyle and external stalk with transverse striae. Zooid 90 μm long × 15 μm wide and extends up to one third of its length beyond aperture. Macronucleus short and lies longitudinally in centre of zooid. Pellicular striations inconspicuous.

HABITAT. Freshwater, originally found attached to *Entomostraca* (Stein, 1867); also occurs as an epizoite of the crayfish *Astacus leptodactylus* and *Cambarus affinis* (Krucinska and Simon, 1968).

Cothurnia curvula Entz (1876), 1884

Cothurnia imberbis var. *curvula* Entz, 1876

DESCRIPTION (Figs 71–73). Lorica 60 μm long × 30 μm wide, occasionally with three centrally located annular furrows. Aperture 15 μm in diameter. External stalk short with bulbous thickening at its point of attachment to lorica. Mesostyle and endostyle absent. Zooid 60 μm long × 8–10 μm wide and extends just beyond aperture. Macronucleus straight and lies longitudinally in zooid. Pellicular striations inconspicuous.

HABITAT. Marine, found attached to harpacticoid copepods from the Gulf of Neapel (Entz, 1884).

Cothurnia cyathiforme Stiller, 1939

Cothurnia compressa var. *cyathiformis* Felinska, 1965
Sincothurnia cyathiformis (Stiller, 1939) Jankowski, 1985

DESCRIPTION (Figs 76–78). Lorica asymmetrical, 95–100 μm long × 45 μm wide. Aperture 30 μm wide and with shallow cleft in border. External stalk and endostyle short; mesostyle broad with conspicuous longitudinal striae. Two zooids per lorica, each 70 μm long when contracted. Pellicular striations conspicuous.

HABITAT. Marine.

NOTE. The data above are based on observations of contracted specimens only. Uncontracted specimens of *C. cyathiforme* have yet to be described.

Cothurnia cyclopis Kahl, 1933

DESCRIPTION (Fig. 79). Lorica 60 μm long × 25 μm wide with irregular ridges and furrows. External stalk slender 15 μm long; mesostyle short and broad; endostyle short and slender. Zooid 80 μm long × 20 μm wide, extending up to one third of its length beyond aperture. Pellicular striations inconspicuous.

HABITAT. Marine, originally found attached to harpacticoid copepods (Kahl, 1933).

Cothurnia cylindrica Sommer, 1951

DESCRIPTION (Fig. 80). Lorica cylindrical, 61 μm long × 29 μm wide. Aperture 27 μm in diameter. External stalk 5 μm long with a broad cylindrical swelling at its point of attachment to lorica. Two zooids per lorica, each 81–95 μm long × 13–16 μm wide and extending up to one fifth of its length beyond

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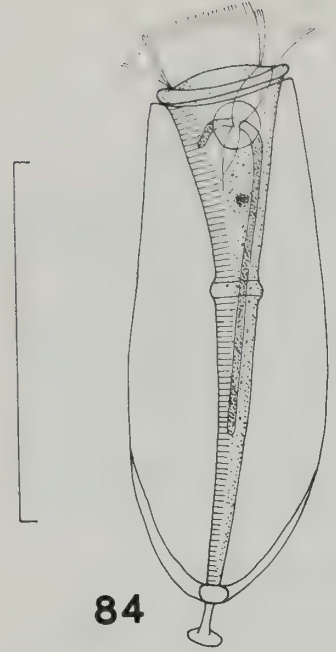
Fig. 74 *Cothurnia cohni*, after Kahl, 1935, bar = 50 μm.
Fig. 75 *Cothurnia cordylophorae*, after Kahl, 1935, bar = 100 μm.
Figs 76–78 *Cothurnia cyathiforme*; figs 76 & 77 after Stiller, 1939, bar = 50 μm; fig. 78 after Felinska, 1965 (called *Cothurnia compressa* var. *cyathiformis*).
Fig. 79 *Cothurnia cyclopis*, after Kahl, 1933, bar = 50 μm.
Fig. 80 *Cothurnia cylindrica*, after Sommer, 1951, bar = 50 μm.
Figs 81 & 82 *Cothurnia cypridicola*, after Kahl, 1933, bar = 50 μm.
Fig. 83 *Cothurnia cytherideae*, after Kahl, 1933, bar = 50 μm.



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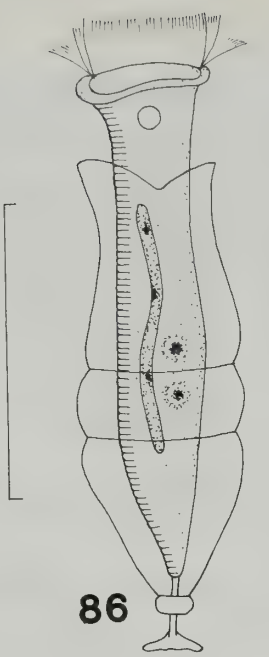

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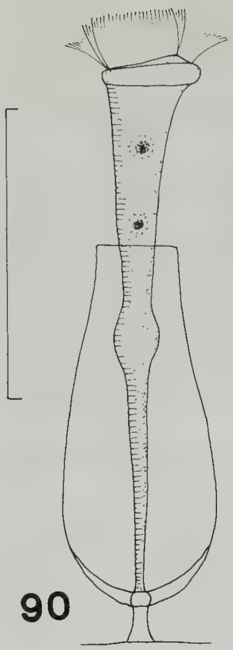

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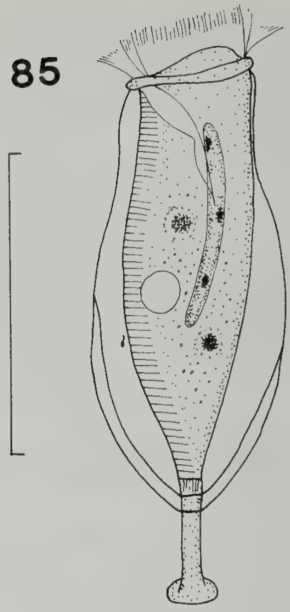

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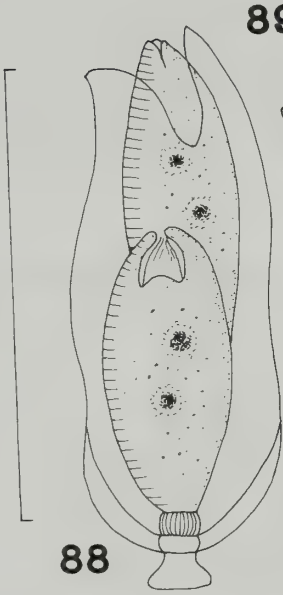

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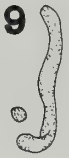

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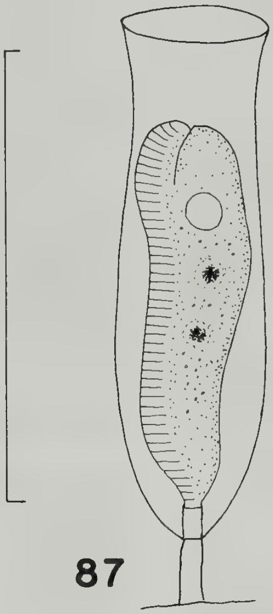

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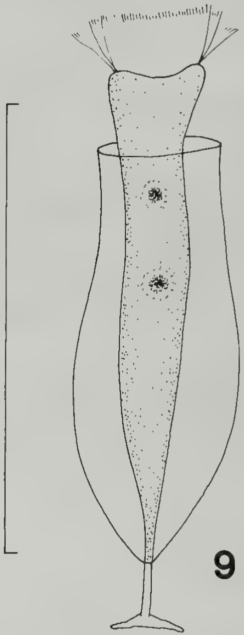

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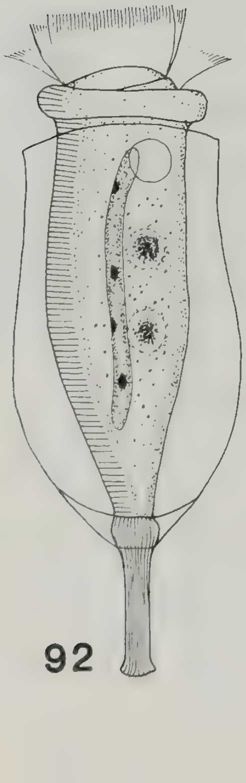

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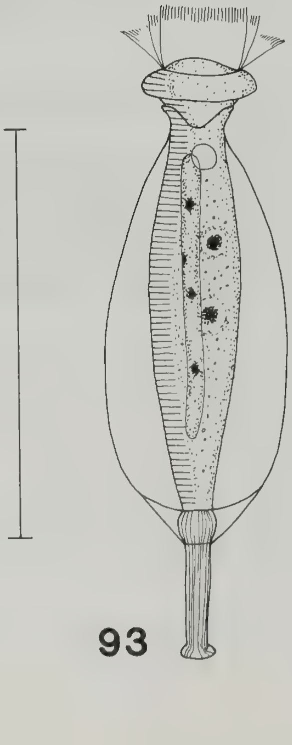

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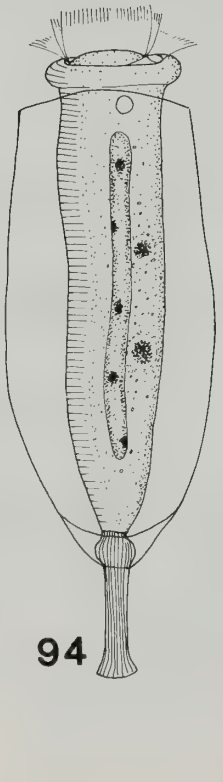

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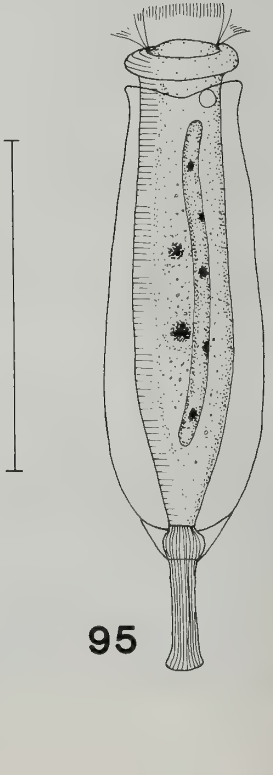


95

aperture. Peristomial lip 20–22 μm in diameter. Disc obliquely elevated. CV situated just below peristome. Pellicular striations inconspicuous.

HABITAT. Freshwater, originally found attached to *Enteromorpha intestinalis* (Sommer, 1951).

NOTE. If coloniality (*sensu* Jankowski, 1985) is accepted as a generic character, this species should be included in the genus *Sincothurnia*.

Cothurnia cypridicola Kahl, 1933

DESCRIPTION (Figs 81 & 82). Lorica 50–60 μm long ×20–25 μm wide and with irregular ridges and furrows. Aperture ovoid when viewed from above, 25 μm × 15 μm. External stalk short; mesostyle and endostyle short and broad. Zooid elongate, 70–80 μm long × 10–12 μm wide and extending up to one third of its length beyond aperture. Pellicular striations inconspicuous.

HABITAT. Marine or brackish water, originally found on cyprids (Kahl, 1933); also found on the gastropods *Hydrobia ulvae* and *H. jenkinsi*, and on the ostracod *Cyprideis litoralis* (Precht, 1935).

Cothurnia cytherideae Kahl, 1933

DESCRIPTION (Fig. 83). Lorica cylindrical, 70 μm long × 35 μm wide and rounded posteriorly. Aperture 30 μm in diameter. External stalk slender 35 μm long; mesostyle broad; endostyle slender. Zooid ovoid when contracted, 45 μm long × 20 μm wide. Macronucleus curved and lies longitudinally in zooid. Pellicular striations inconspicuous.

HABITAT. Marine, originally found as an epibiont of the hydroid *Cytheridea* (Kahl, 1933).

Cothurnia elegans Stiller, 1940

DESCRIPTION (Fig. 84). Lorica 65–75 μm long × 30 μm wide. Aperture 20 μm in diameter. External stalk 6–10 μm long; mesostyle short and broad; endostyle absent. Zooid 65–75 μm long × 10–30 μm wide with centrally located annular ridge. Zooid just reaches aperture when extended. Peristome 30 μm in diameter. CV large and situated just below peristome. Macronucleus curved anteriorly and lies longitudinally in the body. Pellicular striations conspicuous.

HABITAT. Marine or freshwater, originally found attached to algae from Lake Holstein (Stiller, 1940); also isolated from laboratory aquaria at Plymouth attached to green algae (Felinska, 1965).

Cothurnia elongata Felinska, 1965

Sincothurnia elongata (Felinska, 1965) Jankowski, 1985

DESCRIPTION (Fig. 85). Lorica 150 μm long × 65 μm wide. Aperture 40–45 μm wide. External stalk 30–40 μm long; mesostyle short; endostyle short with conspicuous longitudinal striae. Zooid 150 μm long × 45 μm wide and just reaches aperture when extended. Peristomial lip 45 μm in diameter. CV lies near the centre of body. Macronucleus straight and lies longitudinally in anterior part of zooid. Pellicular striations conspicuous.

HABITAT. Marine, originally isolated from laboratory aquaria at Plymouth (Felinska, 1965).

Cothurnia entzi Kahl, 1933

Cothurnia nodosa Entz, 1884

DESCRIPTION (Fig. 86). Lorica 70–80 μm long × 30–40 μm wide and with two or three centrally located annular furrows. Aperture border with shallow cleft. External stalk slender, up to 50 μm long and with bulbous swelling at point of attachment to lorica; endostyle short and slender; mesostyle absent. Two zooids per lorica, each 85–90 μm long × 20 μm wide and extending up to one quarter of its length beyond aperture. Peristomial lip well developed, 25 μm in diameter. CV situated near centre of infundibulum. Macronucleus straight or slightly curved and lies longitudinally in zooid. Pellicular striations conspicuous with convex ribbing between striations.

HABITAT. Marine.

Cothurnia fecunda Stokes, 1893

DESCRIPTION (Fig. 87). Lorica cylindrical, 110 μm long × 35 μm wide. Aperture 30 μm in diameter. External stalk 15 μm long; endostyle inconspicuous; mesostyle absent. Two zooids per lorica, each 80 μm long × 20 μm wide when contracted, although only one zooid may contract completely at any time. Pellicular striations conspicuous.

HABITAT. Brackish water, originally found attached to filamentous algae in North American canal water (Stokes, 1893).

NOTE. If coloniality (*sensu* Jankowski, 1985) is accepted as a generic character, this species should be included in the genus *Sincothurnia*. Uncontracted specimens of *C. fecunda* have yet to be described.

Cothurnia felinska (Felinska, 1965) n. sp.

Cothurnia compressa var. *compressula* Felinska, 1965

DESCRIPTION (Figs 88 & 89). Lorica 110 μm long × 40 μm

Fig. 84 *Cothurnia elegans*, after Stiller, 1940, bar = 50 μm.
Fig. 85 *Cothurnia elongata*, after Felinska, 1965, bar = 100 μm.
Fig. 86 *Cothurnia entzi*, after Entz, 1884, bar = 50 μm (called *Cothurnia nodosa*).
Fig. 87 *Cothurnia fecunda*, after Stokes, 1893, bar = 100 μm.
Figs 88 & 89 *Cothurnia felinska*, after Felinska, 1965 (called *Cothurnia compressa* var. *compressula*); fig. 88 bar = 100 μm; fig. 89 nuclei.
Fig. 90 *Cothurnia fibripes*, after Kahl, 1933, bar = 50 μm.
Fig. 91 *Cothurnia floscularia*, after Perty, 1852, bar = 100 μm.
Figs 92 & 93 *Cothurnia gammari*, after Precht, 1935, bar = 50 μm; fig. 92 ventral view; fig. 93 lateral view.
Figs 94 & 95 *Cothurnia halacaricola*, after Precht, 1935, bar = 50 μm; fig. 94 ventral view; fig. 95 lateral view.

wide with irregular ridges and furrows. Aperture 25 μm wide with two deep clefts in border. External stalk short and broad; mesostyle short; endostyle short and broad with conspicuous longitudinal striae. Two zooids per lorica, each 60–100 μm long × 20–25 μm wide when contracted. Macronucleus lies longitudinally in zooid with posterior end curved upwards. Pellicular striations conspicuous.

HABITAT. Marine, originally found attached to algae from marine aquaria at Plymouth (Felinska, 1965).

NOTE. Felinska (1965) called this organism *Cothurnia compressa* var. *compressula* because it possesses features common to both *C. compressa* Claparede and Lachmann, 1858 and *C. compressula* Kahl, 1935. However it also differs from both of these taxa in terms of its nuclear shape, mesostyle and the longitudinal striae on the endostyle. This last feature, along with the shape of the aperture, serves to separate *C. felinska* from another similar species, *C. cyathiforme* Stiller, 1939.

Cothurnia fibripes Kahl, 1933

DESCRIPTION (Fig. 90). Lorica 60 μm long × 30 μm wide, rounded posteriorly and with irregular ridges and furrows. Aperture 15 μm in diameter. External stalk short and broad; mesostyle broad and with conspicuous longitudinal striae; endostyle absent. Zooid elongate, 90 μm long × 10 μm wide, extending up to one third of its length beyond aperture, and with a centrally located annular ridge. Peristome 15–20 μm in diameter. Pellicle with fine striations.

HABITAT. Marine, originally isolated from laboratory aquaria at Kiel (Kahl, 1933).

Cothurnia floscularia Perty, 1852

DESCRIPTION (Fig. 91). Lorica 85 μm long × 40 μm wide. Aperture 30 μm in diameter. External stalk slender, 8 μm long; mesostyle and endostyle absent. Zooid 90 μm long × 20 μm wide, extending just beyond aperture. Pellicular striations inconspicuous.

HABITAT. Freshwater.

Cothurnia gammari Precht, 1935

Sincothurnia gammari (Precht, 1935) Jankowski, 1985

DESCRIPTION (Figs 92 & 93). Lorica compressed dorso-ventrally, 53–55 μm long × 25–34 μm wide, occasionally with irregular ridges and furrows. Aperture ovoid when viewed from above, 25 μm × 10 μm. External stalk 10–20 μm long; mesostyle short and broad; endostyle absent. Mesostyle and external stalk with conspicuous longitudinal striae. Zooid 65 μm long × 13–22 μm wide, reaching just beyond aperture when extended. Peristomial lip well developed, 15–20 μm in diameter. Disc obliquely elevated. Macronucleus situated longitudinally in zooid, usually curved at both ends. Pellicular striations conspicuous.

HABITAT. Marine, originally found attached to *Gammarus locusta* (Precht, 1935); also found attached to *G. oceanicus* and *G. duebeni* (Fenchel, 1965).

Cothurnia halacaricola Precht, 1935

DESCRIPTION (Figs 94 & 95). Lorica 70 μm long × 23–35 μm wide. Aperture ovoid 28 μm × 17 μm. External stalk 15 μm long; mesostyle short and broad; endostyle inconspicuous. All three stalks with conspicuous longitudinal striae. Zooid cylindrical, 70 μm long × 15 μm wide and reaches just beyond aperture. Peristomial lip well developed, 20 μm in diameter. CV situated just below peristome. Macronucleus straight and lies longitudinally in body. Pellicular striations conspicuous.

HABITAT. Marine, originally found as an epibiont of the halacarid *Copidognathus fabriciusi* (Precht, 1935).

Cothurnia harpactici Kahl, 1933

DESCRIPTION (Figs 96 & 97). Lorica cylindrical, 75–88 μm long × 28–35 μm wide, occasionally with three or four annular ridges and furrows. Aperture 30 μm in diameter. External stalk 15 μm long and sometimes curved; mesostyle short and broad; endostyle short. All three stalks with conspicuous longitudinal striae. Zooid 105 μm long × 17–20 μm wide, extending up to one fifth of its length beyond aperture. Peristomial lip 20 μm in diameter. Macronucleus lies longitudinally in body, proximal end slightly curved. Pellicular striations conspicuous.

HABITAT. Marine, originally found as an epizoite of harpacticoid copepods (Kahl, 1933); also found by Precht (1935) on the harpacticoids *Cletocamptus confluens* and *Mesochra lillgeborgi*.

Cothurnia inclinans Felinska, 1965

DESCRIPTION (Fig. 98). Lorica compressed dorso-ventrally, 57 μm long × 40 μm and with irregular ridges and furrows. Aperture 25 μm wide with a deep cleft in each lateral border. External stalk long and slender with a distinct swelling at point of attachment to lorica; mesostyle and endostyle absent. Zooid 65 μm long × 25 μm wide, extending up to one third of its length beyond aperture. Peristome 40 μm in diameter.

Figs 96 & 97 *Cothurnia harpactici*, after Precht, 1935, bar = 100 μm; fig. 96 ventral view; fig. 97 lateral view.

Fig. 98 *Cothurnia inclinans*, after Felinska, 1965, bar = 50 μm.

Fig. 99 *Cothurnia inflata*, after Stokes, 1893, bar = 50 μm.

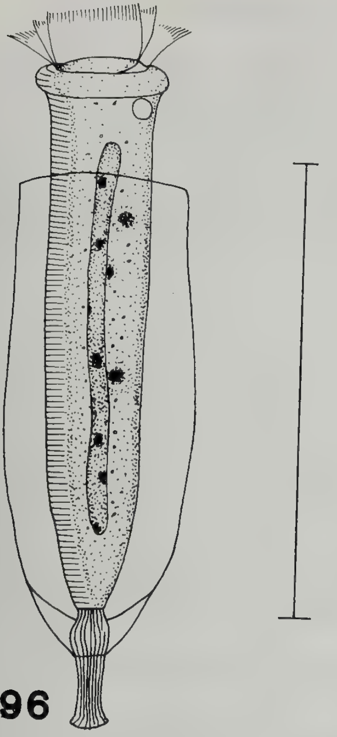
Fig. 100 *Cothurnia inflecta*, after Stiller, 1939, bar = 50 μm.

Figs 101–103 *Cothurnia innata*; fig. 101 after Müller, 1786, bar = 50 μm; figs 102 & 103, after Hofker, 1930.

Fig. 104 *Cothurnia irregularis*, after Fromentel, 1874, bar = 50 μm.

Figs 105 & 106 *Cothurnia lapponum*; fig. 105 after Penard, 1922, bar = 100 μm; fig. 106 after Wang, 1977 (called *Cothurnia lapponum naidongensis*).

Fig. 107 *Cothurnia longipes*, after Mereschkowsky, 1879, bar = 100 μm.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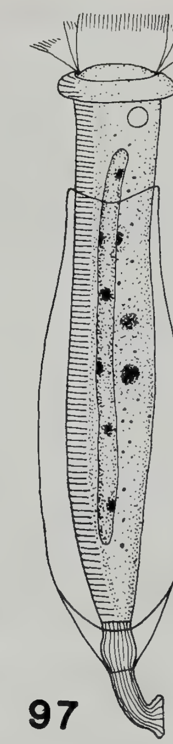
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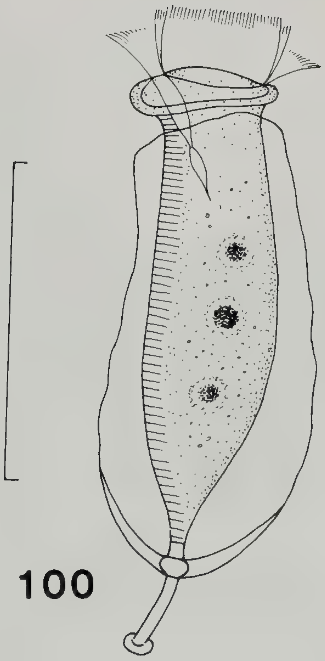
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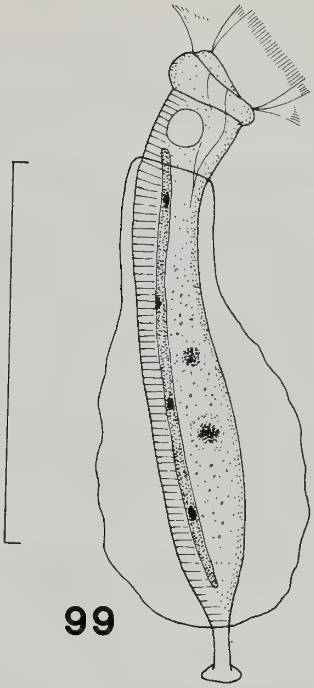
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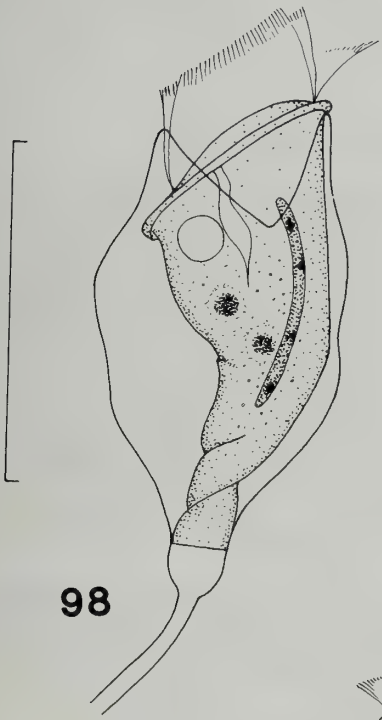
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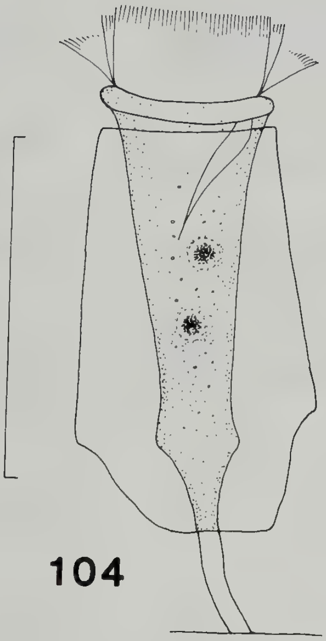
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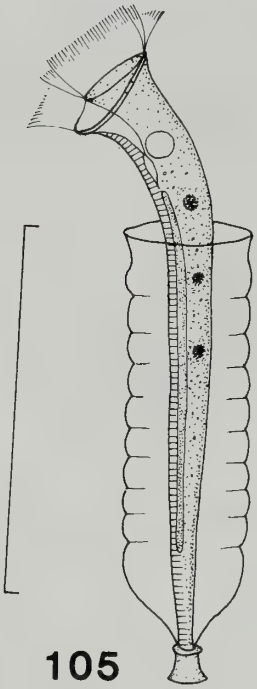
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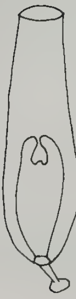
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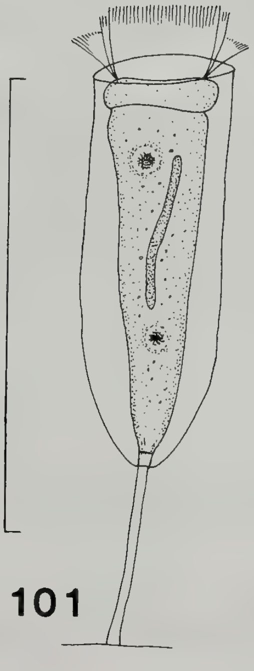
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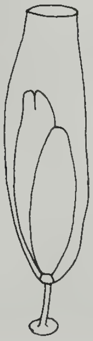
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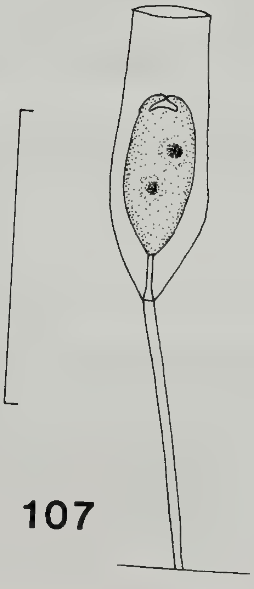
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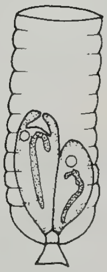
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Disc convex. CV situated just below peristome. Macronucleus straight and lies in upper two thirds of zooid. Pellicular striations inconspicuous.

Habitat. Marine, originally found attached to algae from marine aquaria at Plymouth (Felinska, 1965).

Cothurnia inflata Stokes, 1893

Description (Fig. 99). Lorica 60 μm long × 30 μm wide, rounded posteriorly and with irregular ridges and furrows. External stalk short and slender; endostyle short and with conspicuous longitudinal striae; mesostyle absent. Zooid 75 μm long × 12 μm wide, extending up to one fifth of its length beyond aperture. Peristomial lip 15 μm in diameter. Disc obliquely elevated. CV situated just below peristome. Macronucleus straight, extending almost entire zooid length. Pellicle with fine striations.

Habitat. Brackish water, originally found attached to filamentous algae from Coney Island, New York (Stokes, 1893).

Cothurnia inflecta Stiller, 1939

Description (Fig. 100). Lorica 70 μm long × 35 μm wide with irregular ridges and furrows. Aperture 25 μm in diameter. External stalk slender, 10 μm long; mesostyle short and broad; endostyle short and slender. Zooid 70 μm long × 20 μm wide and reaches just beyond aperture. Peristomial lip 25 μm in diameter. Macronucleus vermiform. Pellicular striations conspicuous.

Habitat. Marine, originally found attached to green algae from the North Sea near Helgoland (Stiller, 1939).

Note. The original diagram of this species was labelled '*Cothurnia inflexa*' (Stiller, 1939); this is assumed to be a misspelling of *C. inflecta*.

Cothurnia innata Müller, 1786

Cothurnia hofkeri (Hofker, 1930) Kahl, 1933

Description (Figs 101–103). Lorica cylindrical, 40–100 μm long × 20–27 μm wide. Aperture 10–15 μm in diameter. External stalk 20 μm long; endostyle short and broad; mesostyle absent. Two zooids per lorica, each 40–50 μm long × 10–15 μm wide and not reaching as far as aperture. Peristomial lip well developed, 15 μm in diameter. Pellicular striations inconspicuous.

Habitat. Marine, found by Hofker (1930) attached to *Hydrobia* spp.

Cothurnia irregularis Kent, 1881

Cothurnia nodosa Fromentel, 1874

Description (Fig. 104). Lorica 55 μm long × 35 μm wide, anterior end conical, posterior end broad and rounded. Aperture 20 μm in diameter. External stalk 10–15 μm long; endostyle short and inconspicuous; mesostyle absent. Zooid 55 μm long × 15 μm wide and extending just beyond aperture. Peristome 20 μm in diameter. Pellicular striations inconspicuous.

Habitat. Freshwater.

Cothurnia kahli Banina and Polyakova, 1977

Description (Fig. 108). Lorica 43–50 μm long × 21–29 μm wide. Aperture 18 μm in diameter. External stalk 3–4 μm long and penetrates lorica wall via special tube. Two zooids per lorica, each 50–56 μm long × 15 μm wide and extends just beyond aperture. Peristome 18 μm in diameter. CV lies just below peristome. Pellicular striations inconspicuous.

Habitat. Freshwater, originally found attached to *Cladophora* (Banina and Polyakova, 1977).

Note. If coloniality (*sensu* Jankowski, 1985) is accepted as a generic character, this species should be included in the genus *Sincothurnia*.

Cothurnia lapponum Penard, 1922

Cothurnia lapponum naidongensis Wang Jiaji, 1977

Description (Figs 105 & 106). Lorica cylindrical 92–116 μm long × 30–49 μm wide and with regular annular furrows along the entire length with exception of posterior end. External stalk 7–8 μm long; mesostyle and endostyle absent. Two zooids per lorica, each 140 μm long × 15 μm wide and extends one quarter of its length beyond aperture. Peristome 25 μm in diameter. CV situated near centre of infundibulum. Macronucleus straight and lies longitudinally in zooid. Micronucleus large, ovoid and lies below posterior end of macronucleus. Pellicle with fine striations.

Habitat. Freshwater, originally found on *Sphagnum* from Haparanda, Sweden (Penard, 1922); also isolated from marsh water at Naidong, Tibet, 400 m above sea level (Wang Jiaji, 1977).

Note. *C. lapponum naidongensis* was described by Wang Jiaji (1977) as a subspecies of *C. lapponum*. Wang Jiaji cited the shape of the lorica as the main difference between the two taxa. However, no description of an uncontracted *C. lapponum naidongensis* was given and no mention was made of the endostyle, which is absent in Penard's animal but appears to

Fig. 108 *Cothurnia kahli*, after Banina and Polyakova, 1977, bar = 50 μm.

Figs 109–111 *Cothurnia lata*, after Kellicott, 1883, bar = 50 μm; fig. 109 ventral view; fig. 110 aperture, anterior view; fig. 111 lateral view.

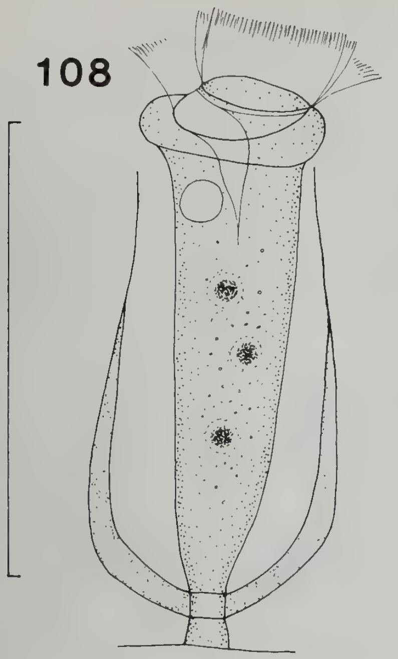
Figs 112–114 *Cothurnia limnoriae*, after Dons, 1928; fig. 112 bar = 50 μm; figs 113 & 114 showing variation in lorica and macronucleus.

Fig. 115 *Cothurnia macrodisca*, after Stiller, 1971, bar = 50 μm.

Fig. 116 *Cothurnia magna*, after Yunfen, 1980, bar = 200 μm.

Fig. 117 *Cothurnia membranoloricata*, after Stiller, 1968, bar = 50 μm.

Figs 118–121 *Cothurnia maritima*; fig. 118 after Felinska, 1965, bar = 50 μm; fig. 119 after Jankowski, 1965 (called *Cothurnia cyathus*); fig. 120 after Andrussowa, 1886 (called *Cothurnia marina*); fig. 121 after Ehrenberg, 1838.



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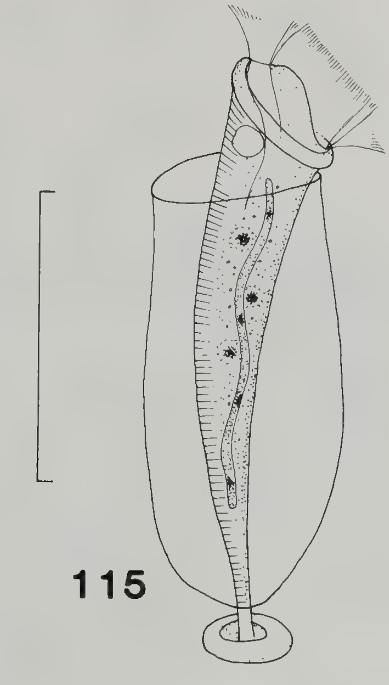

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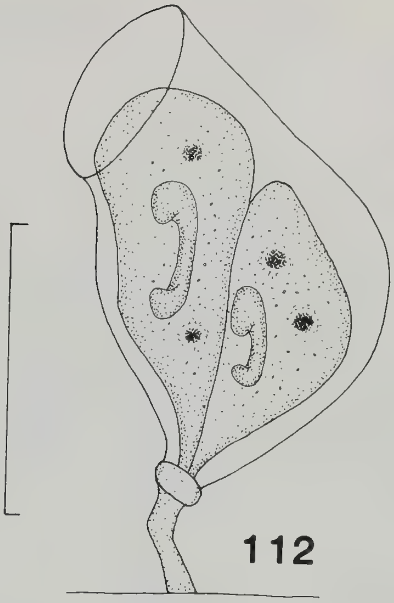

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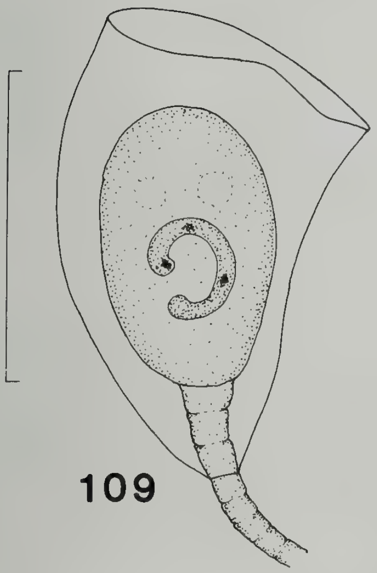

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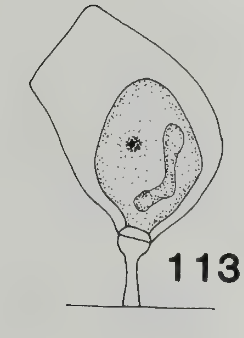

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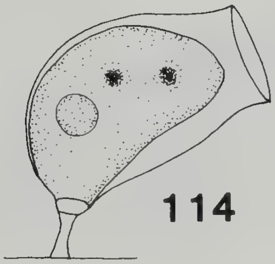

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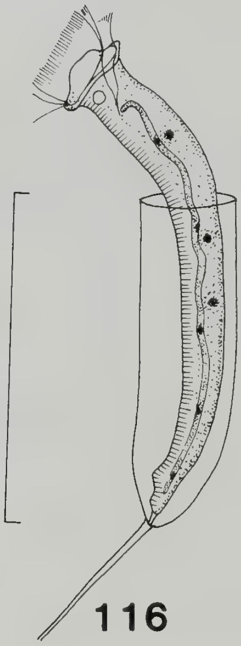

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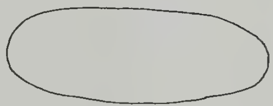

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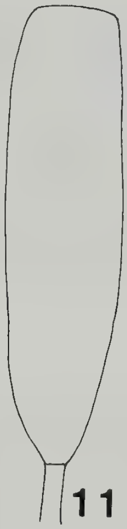

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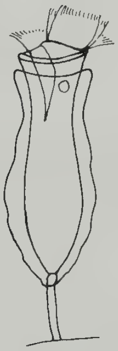

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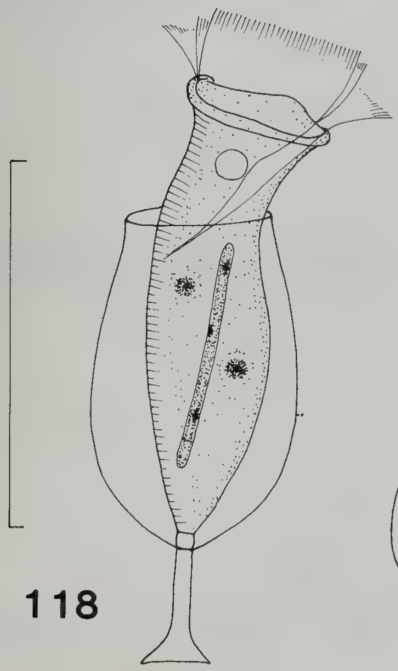

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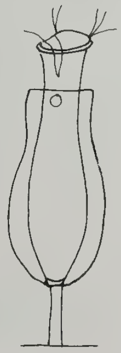

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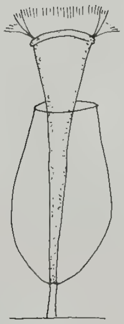

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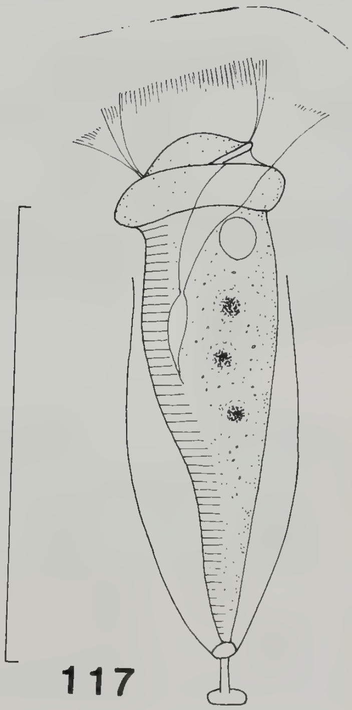

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be present in Wang Jiaji's. Until more data are available there are not considered to be sufficient differences between *C. lapponum* and *C. lapponum naidongensis* for their recognition as separate taxa.

Cothurnia lata Kellicott, 1883

Cothurnia lata (Wailes, 1928) Kahl, 1935

DESCRIPTION (Figs 109–111). Lorica compressed dorso-ventrally, 70 μm long × 40–45 μm wide × 20 μm deep. Aperture elliptical when viewed from above. External stalk 20–25 μm long and curved; endostyle short; mesostyle absent. External stalk and endostyle with transverse furrows. Zooid 70 μm long × 20 μm wide and just reaches aperture. CV situated at base of infundibulum. Macronucleus short, C-shaped and lies in centre of zooid. Pellicular striations inconspicuous.

HABITAT. Freshwater, originally found as an epibiont of the copepod *Diaptomus* (Kellicott, 1883b).

Cothurnia limnoriae Dons, 1928

Tesnotheca limnoriae (Dons, 1928) Jankowski, 1987

DESCRIPTION (Figs 112–114). Lorica curved, 70–90 μm long × 33–40 μm wide. Aperture 30–40 μm in diameter. External stalk 20–40 μm long; mesostyle short and broad; endostyle absent. Two zooids per lorica, each 60 μm long × 40 μm wide. Macronucleus C-shaped, 30 μm long. Pellicular striations inconspicuous.

HABITAT. Marine, originally found as an epizoite of *Limnoria lignorum* (Dons, 1928).

NOTE. Jankowski (1987) erected the genus *Tesnotheca* for *C. limnoriae* on the basis that following binary fission the zooid grows asymmetrically with the peristome inclined to one side, whereas typical *Cothurnia* zooids are symmetrical. The symmetry of the zooid, however, has never previously been used for separating peritrich genera, and furthermore no description or diagram of an uncontracted zooid of *C. limnoriae* has been found in the literature. Therefore, *C. limnoriae* is retained in the genus *Cothurnia*.

Cothurnia longipes Kellicott, 1894

Cothurnia longipes (Mereshkowsky, 1879) Kahl, 1935
Cothurnia nodosa var. *longipes* Mereschkowsky, 1879

DESCRIPTION (Fig. 107). Lorica 100 μm long × 35 μm wide. Aperture 30 μm in diameter. External stalk slender, 100–120 μm long; endostyle slender, 20–40 μm long; mesostyle absent. Zooid 55 μm long × 25 μm wide when contracted. Pellicular striations inconspicuous.

HABITAT. Marine, originally isolated from the White Sea (Mereschkowsky, 1879); also found on sea-weeds and polyzoa from tide pools in North America (Kellicott, 1883a).

NOTE. This taxon was first described by Mereschkowsky (1879) under the name *C. nodosa* var. *longipes*, although it was renamed *C. longipes* by Kahl (1935). In the meantime, however, Kellicott (1894) isolated a similar organism from North America which he called *Cothurnia longipes*. Kellicott (1894) made no reference to Mereschkowsky's (1879) work. The two organisms appear to be synonymous thus solving the problem of homonymy.

Cothurnia macrodisca Stiller

DESCRIPTION (Fig. 115). Lorica 75 μm long × 40 μm wide. Aperture 35 μm in diameter. External stalk 5–6 μm long, attached to substratum via conspicuous ring-like basal disc; mesostyle and endostyle absent. Zooid 90 μm long × 15 μm wide, extending up to one sixth of its length beyond aperture. Peristomial lip well developed, 25 μm in diameter and inclined at angle to main body axis. Disc convex. CV situated just below peristome. Macronucleus vermiform and lies longitudinally in zooid. Pellicle with fine striations.

HABITAT. Freshwater, originally found attached to *Spirogyra* (see Stiller, 1971).

NOTE. The original description of *C. macrodisca* could not be located. Stiller (1971) cited Stiller as the authority for this species but did not give a date or reference.

Cothurnia magna Yunfen, 1980

DESCRIPTION (Fig. 116). Lorica 200 μm long × 56 μm wide, cylindrical and tapering posteriorly towards stalk. Aperture 56 μm in diameter. External stalk 95 μm long × 3 μm wide; endostyle short and slender; mesostyle absent. Zooid elongate, 280–300 μm long × 25 μm wide and extending up to one third of its length beyond aperture. Peristomial lip 52 μm in diameter. Disc convex. CV situated just below peristome. Macronucleus vermiform and extends almost entire body length. Pellicle with fine striations.

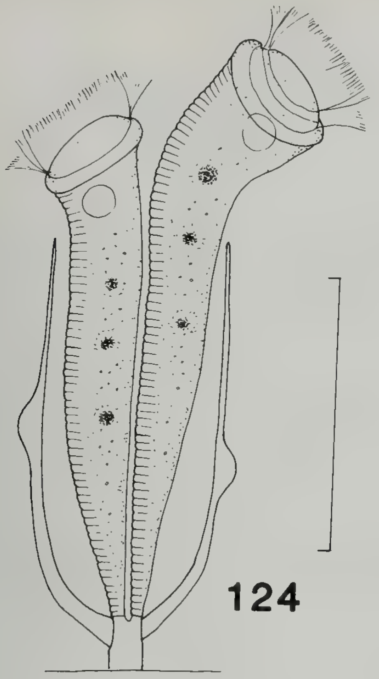
HABITAT. Freshwater, originally isolated from Lake Dong, China (Yunfen, 1980).

Cothurnia maritima Ehrenberg, 1838

Cothurnia cyathus Jaworowski, 1893
Cothurnia marina Andrussowa, 1886

DESCRIPTION (Figs 118–121). Lorica 35–56 μm long × 28–33 μm wide, occasionally with irregular ridges and furrows. Aperture 25 μm × 17 μm. External stalk 10–15 μm long;

Fig. 122 *Cothurnia minutissima*, after Penard, 1914, bar = 50 μm.
Fig. 123 *Cothurnia mobiusi*, after Stiller, 1939, bar = 50 μm.
Fig. 124 *Cothurnia monoannulata*, after Banina and Polyakova, 1977.
Fig. 125 *Cothurnia nereicola*, after Precht, 1935, bar = 50 μm.
Figs 126 & 127 *Cothurnia nitocrae*, after Precht, 1935, bar = 50 μm; fig. 126 ventral view; fig. 127 lateral view.
Figs 128 & 129 *Cothurnia nodosa*; fig. 128 after Claparede and Lachmann, 1858, bar = 50 μm; fig. 129 after Kahl, 1935, bar = 50 μm.
Fig. 130 *Cothurnia obliqua*, after Bock, 1952, bar = 100 μm.
Fig. 131 *Cothurnia oblonga*, after Kahl, 1935, bar = 50 μm.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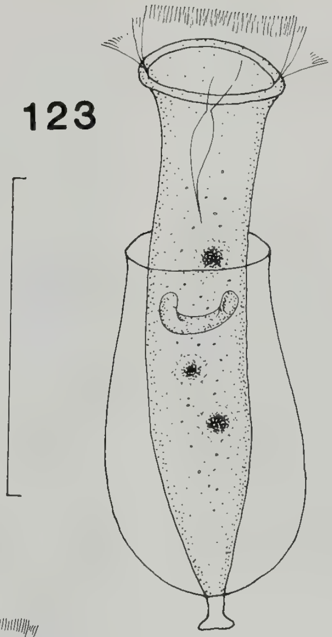
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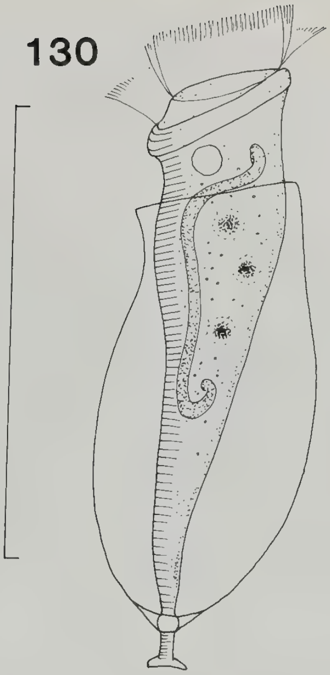
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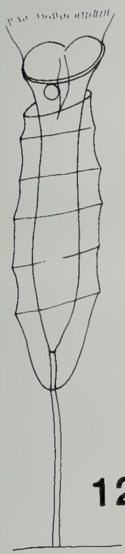
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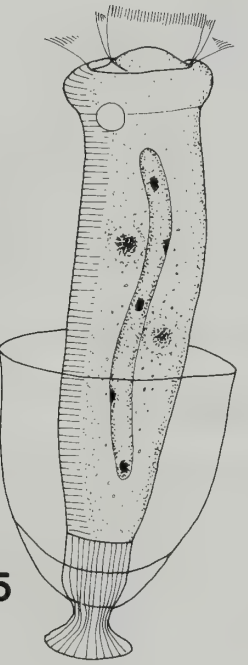
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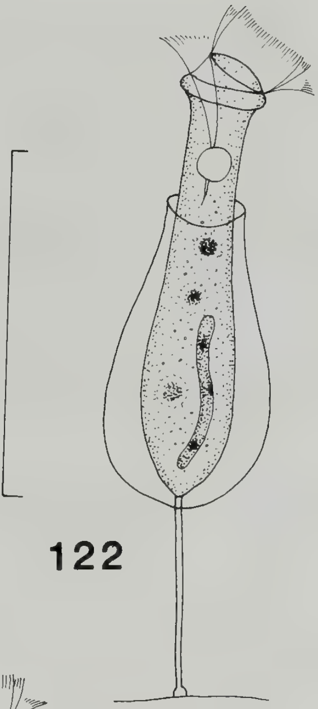
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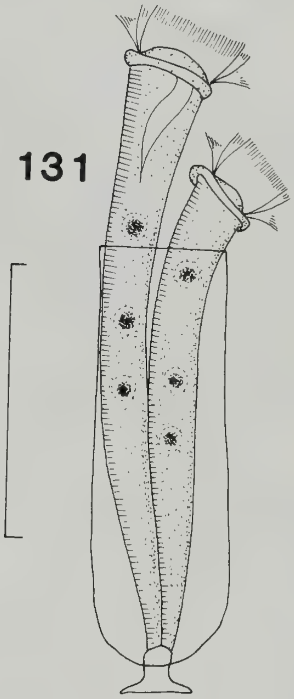
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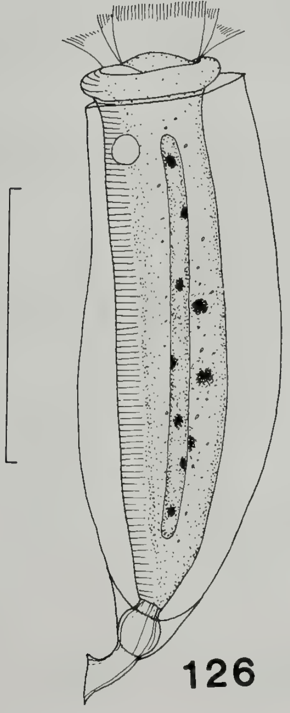
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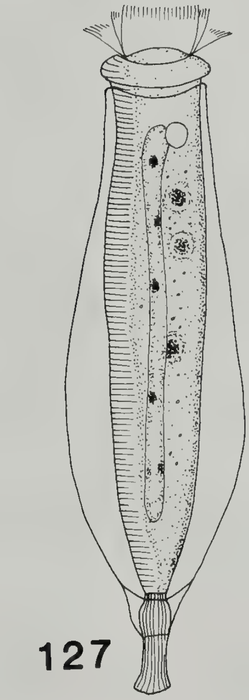
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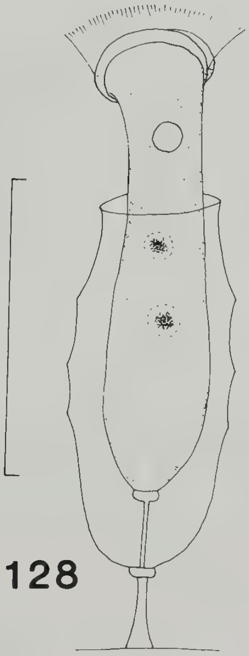
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endostyle short and broad; mesostyle absent. Zooid 60 μm long × 12–15 μm wide, extending up to one third of its length beyond aperture. Peristomial lip 20–25 μm in diameter. CV situated near centre of infundibulum which is about one third zooid length. Macronucleus straight and lies longitudinally in body. Pellicle with fine striations.

HABITAT. Marine, attached to a variety of substrates.

NOTE. Several authors (Quennerstedt, 1865; Andrussowa, 1886; Möbius, 1888; Kahl, 1935; Stiller, 1939; Felinska, 1965) have described cothurnias under this name. The descriptions given by Quennerstedt (1865) and Felinska (1965) conform with Ehrenberg's (1838) original description, whereas those given by Möbius (1888), Kahl (1935) and Stiller (1939) show several differences; *C. maritima sensu* Mobius, 1888 was redescribed by Stiller (1939) under the name *C. mobiusi mihi* (= *C. mobiusi*); *C. sp.* ('bei *maritima*') Kahl, 1935 = *C. obliqua* Bock, 1952; and *C. maritima* Stiller, 1939 possesses a mesostyle whereas *C. maritima* Ehrenberg, 1838 does not.

Cothurnia membranoloricata Stiller, 1968

DESCRIPTION (Fig. 117). Lorica 40–45 μm long × 18–23 μm wide. Aperture 20 μm in diameter. External stalk 8–12 μm long and attached to substrate via basal disc, 4–6 μm in diameter; endostyle short and broad; mesostyle absent. Zooid 55–57 μm long × 12–15 μm wide, extending up to one quarter of its length beyond aperture. Peristomial lip well developed, 5 μm thick × 15–18 μm in diameter. Disc convex. CV lies just below peristome. Pellicle clearly striated with 14–15 striations per 10 μm.

HABITAT. Marine, originally found attached to *Cladophora repens* and *C. heteronema* in Yugoslavian coastal waters (Stiller, 1968).

NOTE. *C. membranoloricata* was found by Viljoen and van As (1983) attached to the alga *Spirogyra*; it was misspelt *C. membraniloricata*.

Cothurnia minutissima (Penard, 1914) Kahl, 1935

Cothurnia sinuata Kahl, 1933
Cothurniopsis minutissima Penard, 1914

DESCRIPTION (Fig. 122). Lorica 35–50 μm long × 18–27 μm wide and rounded posteriorly. Aperture 10–12 μm wide. External stalk slender, 6–17 μm long; endostyle short and slender; mesostyle absent. Zooid 50–55 μm long × 10 μm wide, extending up to one third of its length beyond aperture. Peristomial lip well developed, 10 μm in diameter. Disc convex. CV large and situated near base of infundibulum. Macronucleus straight and lies longitudinally in posterior half of zooid. Pellicle with fine striations.

HABITAT. Freshwater, originally found attached to moss (Penard, 1914); also found on detritus (Kahl, 1935) and on *Enteromorpha intestinalis* (Sommer, 1951).

Cothurnia mobiusi (Möbius, 1888) Stiller, 1939

Cothurnia maritima Möbius, 1888
Cothurnia mobiusi mihi (Möbius, 1888) Stiller, 1939

DESCRIPTION (Fig. 123). Lorica 50 μm long × 30 μm wide. Aperture 20 μm in diameter and sometimes inclined at an angle to main lorica axis. External stalk short; mesostyle and endostyle absent. Zooid 70 μm long × 15 μm wide, extending up to one half of its length beyond aperture. Peristomial lip 20 μm in diameter. CV situated one quarter of way down zooid. Macronucleus C-shaped and lies transversely in centre of zooid. Pellicular striations inconspicuous.

HABITAT. Marine, isolated by Stiller (1939) from the North Sea near Helgoland.

NOTE. Stiller (1939) described a *Cothurnia* which conforms closely with *C. maritima* Möbius (1888) but clearly differs from Ehrenberg's (1838) *C. maritima*. Stiller (1939) called this organism *C. mobiusi mihi*, although the subspecies epithet *mihi* may be disregarded.

Cothurnia monoannulata Banina and Polyakova, 1977

Sincothurnia monoannulata (Banina and Polyakova, 1977) Jankowski, 1985

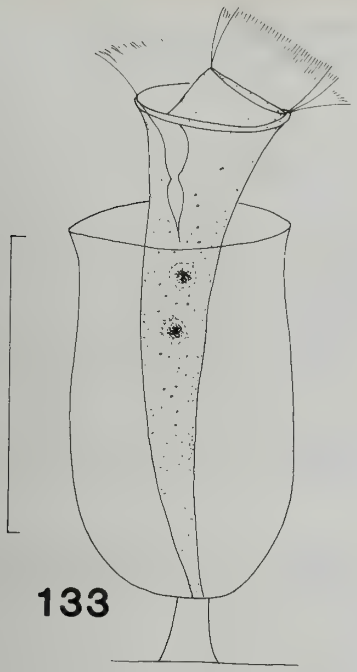
DESCRIPTION (Fig. 124). Lorica cylindrical, 68 μm long × 32 μm wide and with a centrally located annular ridge. Aperture 29 μm in diameter. External stalk 4 μm long and penetrates lorica wall via special tube; mesostyle and endostyle absent. Two zooids per lorica, one larger than the other; larger zooid typically curved anteriorly, 90 μm long × 15 μm wide and extends up to one third of its length beyond aperture; smaller zooid not curved, 80 μm long × 12 μm wide and extends only one sixth of its length beyond aperture. Peristomial lip 18–20 μm in diameter. CV situated just beneath peristome. Pellicular striations conspicuous with convex ribbing between the striations.

HABITAT. Freshwater, originally found attached to *Cladophora* (Banina and Polyakova, 1977).

Cothurnia nereicola Precht, 1935

Semicothurnia nereicola (Precht, 1935) Jankowski, 1976

Fig. 132 *Cothurnia ovalis*, after Kahl, 1933, bar = 50 μm.
Figs 133 & 134 *Cothurnia ovata*, after Fromentel, 1874; fig. 133 bar = 100 μm; fig. 134 macronucleus.
Fig. 135 *Cothurnia oviformis*, after Banina and Polyakova, 1977, bar = 50 μm.
Fig. 136 *Cothurnia parva*, after Bock, 1952, bar = 50 μm.
Fig. 137 *Cothurnia parvula*, after Felinska, 1965, bar = 50 μm.
Fig. 138 *Cothurnia patula*, after Fromentel, 1874, bar = 50 μm.
Figs 139 & 140 *Cothurnia peloscolicis*, after Precht, 1935, bar = 50 μm; fig. 139 ventral view; fig. 140 lateral view.
Fig. 141 *Cothurnia plachteri*, after Matthes and Guhl, 1973, bar = 100 μm.
Fig. 142 *Cothurnia plectostyla*, after Stokes, 1885, bar = 100 μm.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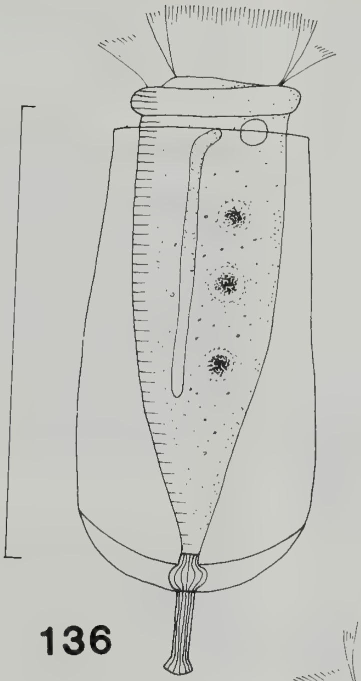
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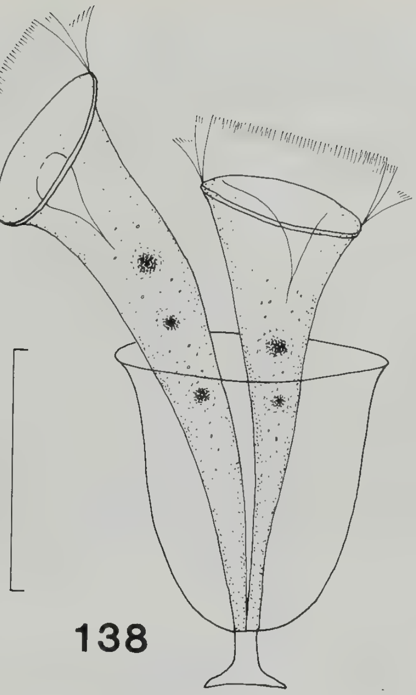
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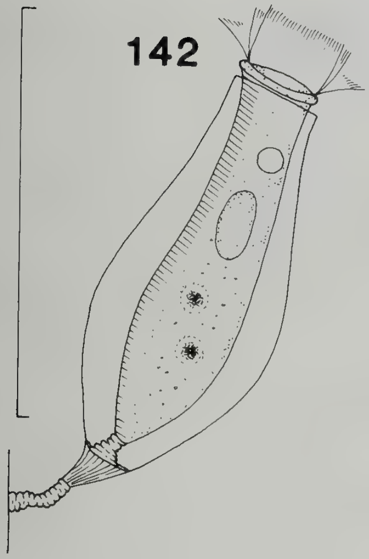
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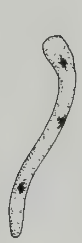
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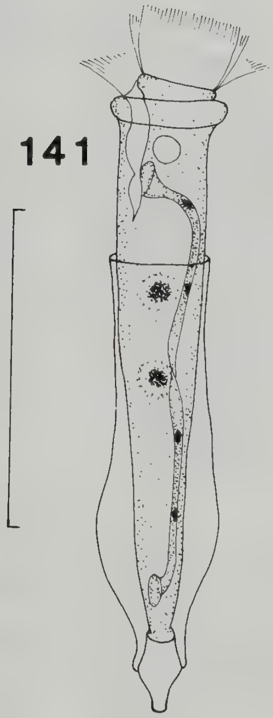
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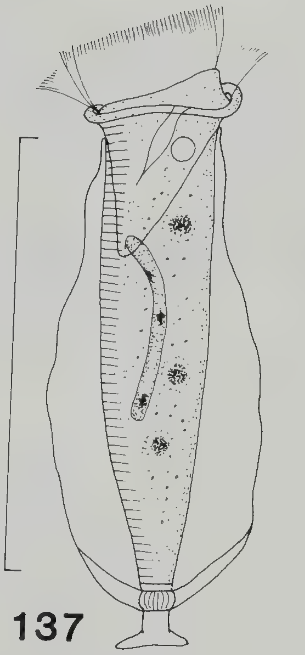
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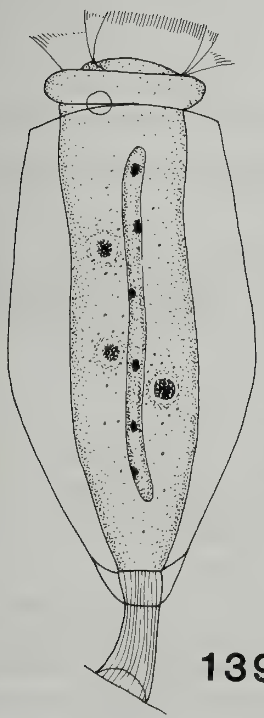
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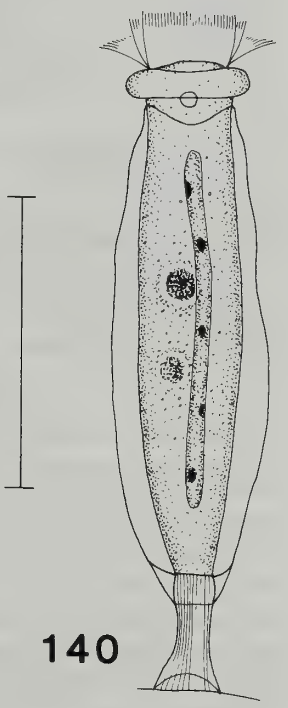
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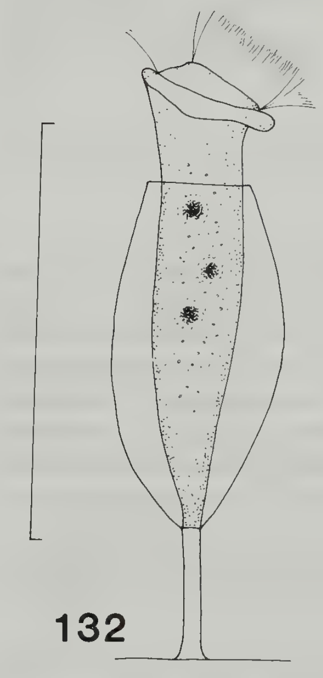
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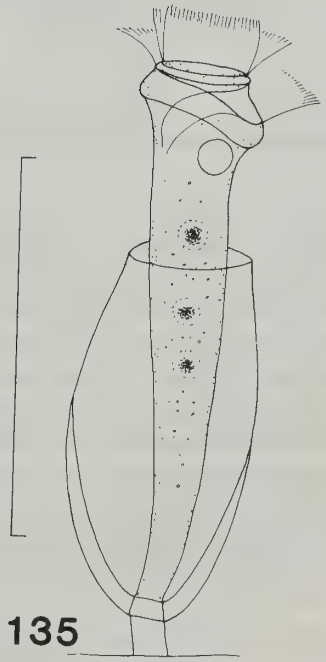
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Description (Fig. 125). Lorica almost hemispherical in shape, 33 μm long × 30 μm wide. Aperture 30 μm in diameter. External stalk short and attached to substratum via basal disc, 10 μm in diameter; mesostyle and endostyle short and broad. All three stalks with continuous longitudinal striae. Zooid 65 μm long × 18 μm wide, extending up to two thirds of its length beyond aperture. Peristomial lip well developed, 20 μm in diameter. Disc convex. CV situated just beneath peristome. Macronucleus straight and lies longitudinally in zooid. Pellicular striations conspicuous.

Habitat. Marine, originally found as an epizoite of the polychaete *Nereis diversicolor* (Precht, 1935).

Note. Jankowski (1976) erected the genus *Semicothurnia* for this species (and for *C. acuta* Levander, 1915) on account of their unusual stalks. The stalk of *C. nereicola* is not, however, considered to be sufficiently distinct for the separation of a new genus.

Cothurnia nitocrae Precht, 1935

Description (Figs 126 & 127). Lorica 93–97 μm long × 30–35 μm wide. Aperture oval when viewed from above, 30 μm × 15 μm. External stalk, mesostyle and endostyle all short with continuous longitudinal striae. Zooid 95 μm long × 20 μm wide and extends just beyond aperture. Peristomial lip 25 μm in diameter. CV situated near anterior end of macronucleus which is straight and 70 μm long. Pellicular striations conspicuous.

Habitat. Marine, originally found as an epizoite of the harpacticoid copepod *Nitoura spinipes* (Precht, 1935).

Cothurnia nodosa Claparede and Lachmann, 1858

Cothurnia sahrhagei (Sahrhage) Kahl, 1933

Description (Figs 128 & 129). Lorica 58 μm long × 26 μm wide and with one or more annular ridges. Aperture 20 μm in diameter. External stalk slender, 15–55 μm long; endostyle slender; mesostyle absent. Two zooids per lorica, each 70 μm long × 15–18 μm wide and extending up to one third of its length beyond aperture. Peristomial lip 20 μm in diameter. CV situated beneath the peristome. Pellicle with fine striations.

Habitat. Marine, originally found attached to algae (Claparede and Lachmann, 1858).

Cothurnia obliqua Bock, 1952

Cothurnia sp. Kahl, 1933

Description (Fig. 130). Lorica 95–96 μm long × 44–45 μm wide. Aperture 37–38 μm in diameter. External stalk 5–7 μm long; mesostyle short and broad; endostyle short and inconspicuous. Zooid 110–115 μm long × 28–30 μm wide, extending up to one fifth of its length beyond aperture. Peristomial lip 35 μm in diameter and inclined at an angle to main zooid axis. CV situated just below peristome. Macronucleus vermiform and curved at both ends. Pellicle with fine striations.

Habitat. Brackish water, found by Kahl (1933) attached to green algae, and by Bock (1952) attached to *Ceramium diapharum*, both at Kiel.

Note. Kahl (1935) described a cothurnid (*Cothurnia* spec.) which he considered to be closely related to *C. maritima* Ehrenberg, 1838. Bock (1952) subsequently isolated *C. obliqua* from the same location, noting the similarity between his and Kahl's (1933) organisms. The two are considered synonymous.

Cothurnia oblonga Kahl, 1935

Description (Fig. 131). Lorica 71–82 μm long × 30–33 μm wide. Aperture 28–30 μm in diameter. External stalk 5 μm long; endostyle short and broad; mesostyle absent. Two zooids per lorica, 90–110 μm long × 18 μm wide. One zooid typically larger than the other, the larger zooid extending up to one third of its length beyond aperture while the smaller one extends only one fifth. CV situated just below peristome. Macronucleus straight, about 70 μm long. Pellicular striations conspicuous.

Habitat. Freshwater, attached to a variety of plant and animal substrates including *Lemna*, *Cladophora* and *Enteromorpha intestinalis* (Kahl, 1935; Sommer, 1951).

Note. *C. oblonga* was redescribed by Sommer (1951).

Cothurnia ovalis (Wailes, 1928) Kahl, 1933

Cothurnia innata Wailes, 1928

Description (Fig. 132). Lorica 40 μm long × 22 μm wide. Aperture oval when viewed from above, 27 μm × 14 μm. External stalk up to 27 μm long; mesostyle and endostyle absent. Zooid 50–58 μm long × 12–18 μm wide, extending up to one third of its length beyond aperture. Peristomial lip 22 μm in diameter. Macronucleus short, curved and lies longitudinally in centre of zooid. Pellicular striations inconspicuous.

Habitat. Marine, originally isolated from Departure Bay, Vancouver (Wailes, 1928).

Cothurnia ovata Dujardin, 1841

Cothurniopsis ovata (Dujardin, 1841) Zelinka, 1928

Description (Figs 133 & 134). Lorica cylindrical, 125 μm long × 75 μm wide. Aperture 75 μm in diameter. External stalk short and broad; mesostyle and endostyle absent. Zooid 175–200 μm long × 25 μm wide, extending up to one third of its length beyond aperture. Peristomial lip 50 μm in diameter. Macronucleus elongate. Pellicular striations inconspicuous.

Habitat. Freshwater, originally found attached to *Conferva* (Fromentel, 1874).

Note. Zelinka (1928) transferred *C. ovata* to *Cothurniopsis* (= *Cothurnopsis*) Entz, 1884, but with the submergence of *Cothurnopsis* by Kahl (1935), this species returned to the genus *Cothurnia*.

Cothurnia oviformis Banina and Polyakova, 1977

Description (Fig. 135). Lorica asymmetric with one side flattened, 48 μm long × 22 μm wide and tapers at both ends. Aperture 16 μm wide. External stalk 5 μm long × 4 μm wide and penetrates lorica wall via special tube; mesostyle and endostyle absent. Zooid 73 μm long × 12 μm wide, extending up to one half of its length beyond aperture. Peristomial lip 15 μm in diameter. CV situated just below peristome. Pellicular striations inconspicuous.

HABITAT. Freshwater, originally found attached to *Cladophora* (Banina and Polyakova, 1977).

Cothurnia parva Bock, 1952

DESCRIPTION (Fig. 136). Lorica 46–50 μm long × 30–34 μm wide. Aperture 23–25 μm in diameter. External stalk 11–14 μm long; mesostyle short and broad; endostyle inconspicuous. All three stalks with conspicuous longitudinal striae. Zooid 49–54 μm long × 17 μm wide, extending just beyond aperture. Peristomial lip 19–21 μm in diameter. CV situated just below peristome. Macronucleus straight and situated in upper two thirds of zooid. Pellicular striations conspicuous.

HABITAT. Brackish water, originally found attached to *Ceramium diaphanum* (Bock, 1952).

Cothurnia parvula Felinska, 1965

DESCRIPTION (Fig. 137). Lorica 50–62 μm long × 24 μm wide with irregular ridges and furrows. Aperture 15 μm wide and with deep cleft in border. External stalk, mesostyle and endostyle all short and broad; mesostyle with conspicuous longitudinal striae. Zooid 55 μm long × 13 μm wide, extending just beyond aperture. Peristomial lip 17 μm in diameter. CV small and situated just below peristome. Macronucleus 20 μm long and lies longitudinally in centre of zooid. Pellicular striations conspicuous.

HABITAT. Marine, originally found attached to algae from laboratory aquaria at Plymouth (Felinska, 1965).

Cothurnia patula Fromentel, 1874

Sincothurnia patula (Fromentel, 1874) Jankowski, 1985

DESCRIPTION (Fig. 138). Lorica 55 μm long × 45 μm wide. Aperture 55 μm in diameter. External stalk short and broad; mesostyle and endostyle absent. Two zooids per lorica, each 110 μm long × 20 μm wide and extending up to one half of its length beyond aperture. Peristomial lip 40 μm in diameter. Pellicular striations inconspicuous.

HABITAT. Freshwater, originally found attached to algae (Fromentel, 1874).

Cothurnia peloscolicis Precht, 1935

DESCRIPTION (Figs 139 & 140). Lorica compressed dorsoventrally, 81 μm long × 27–41 μm wide. Aperture oval when viewed from above, 15 μm × 33 μm. External stalk 20 μm long; mesostyle short and broad; endostyle absent. External stalk and mesostyle with conspicuous longitudinal striae. Zooid 80 μm long × 18–22 μm wide, extending just beyond aperture. Peristomial lip 27 μm in diameter. CV small and situated in peristomial region. Macronucleus straight, 50 μm long. Pellicular striations inconspicuous.

HABITAT. Marine, originally found as an epizoite of the oligochaete *Peloscolex benedeni* (Precht, 1935).

Cothurnia plachteri Matthes and Guhl, 1973

DESCRIPTION (Fig. 141). Lorica elongate, 127 μm long × 30 μm wide and tapering at posterior end. External stalk short and slender; endostyle broad; mesostyle absent. Zooid 118–170 μm long × 26 μm wide, extending up to one third of its length beyond aperture. Peristomial lip 34 μm in diameter. CV situated just below peristome. Macronucleus elongate and curved at both ends. Pellicular striations inconspicuous.

HABITAT. Freshwater, originally found attached to the crayfish *Astacus fluviatilis* and *A. torrentium* (Matthes and Guhl, 1973).

Cothurnia plectostyla Stokes, 1885

DESCRIPTION (Fig. 142). Lorica 80–100 μm long × 30–40 μm wide. Aperture 15–20 μm wide. External stalk 30 μm long, curved with lateral furrows; mesostyle broad with conspicuous longitudinal striae; endostyle short with irregular lateral furrows. Zooid 90 μm long × 25 μm wide, extending just beyond aperture. Peristomial lip 25 μm in diameter. CV situated one quarter of way down zooid. Macronucleus ovoid, 20 μm long, and lies in centre of zooid. Pellicle with fine striations.

HABITAT. Freshwater, originally found attached to *Canthocamptus* (Stokes, 1885).

Cothurnia propinqua Kahl, 1933

DESCRIPTION (Fig. 143). Lorica 60 μm long × 23 μm wide and tapering posteriorly. Aperture 18 μm in diameter. External stalk 10–15 μm long and with irregular transverse furrows; mesostyle slender; endostyle inconspicuous. Zooid 55 μm long × 10 μm wide, extending just beyond aperture. CV situated near base of infundibulum. Macronucleus short, C-shaped and lies obliquely across central region of zooid. Pellicular striations inconspicuous.

HABITAT. Freshwater.

Cothurnia pupa Eichwald, 1849

DESCRIPTION (Fig. 144). Lorica ovoid, length about ×2 width, and with three distinct centrally located annular ridges. External stalk slender, about one quarter of lorica length. Zooid conical in shape, extending just beyond aperture. Peristomial lip broad. Pellicular striations inconspicuous.

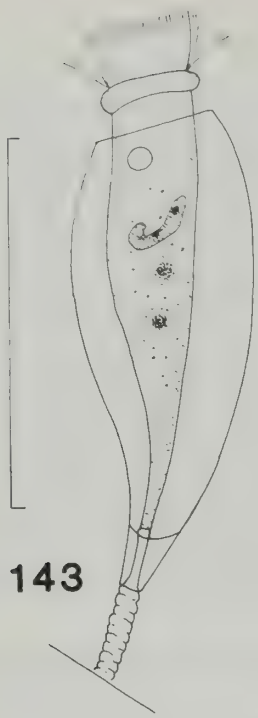
HABITAT. Freshwater.

NOTE. No dimensions were given in the original description and *C. pupa* has never been redescribed.

Cothurnia recurva Claparede and Lachmann, 1858

DESCRIPTION (Figs 145 & 146). Lorica curved and irregular, 45–75 μm long × 17–35 μm wide. Aperture 13–17 μm in diameter. External stalk up to 18 μm long, curved with transverse furrows; endostyle short and broad; mesostyle absent. Zooid 40–70 μm long × 10–17 μm wide, extending just beyond aperture. Diameter of aperture slightly greater than that of lorica. CV small and situated one quarter of way down zooid. Macronucleus straight and lies longitudinally in centre of zooid. Pellicular striations conspicuous.

HABITAT. Marine, found as epizoites of cyclopoid and harpacticoid copepods (Kahl, 1933; Felinska, 1965).



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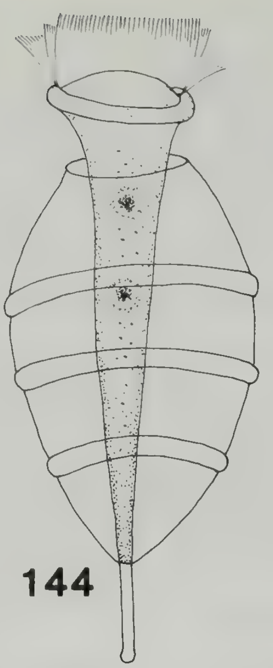

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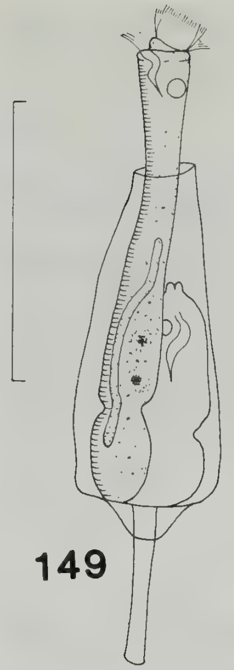

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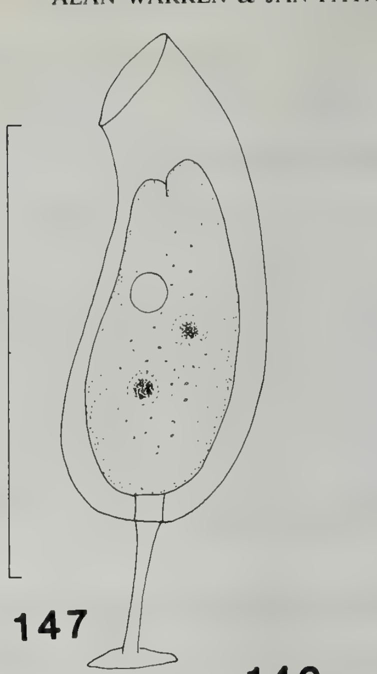

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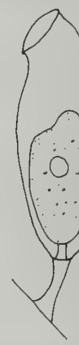

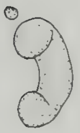

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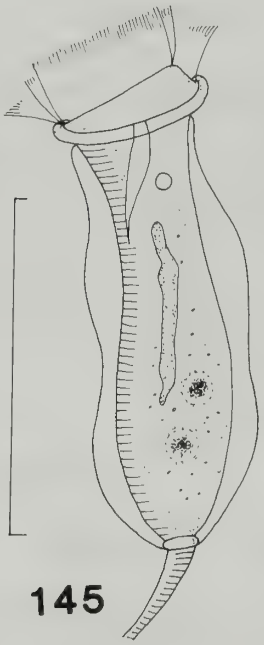

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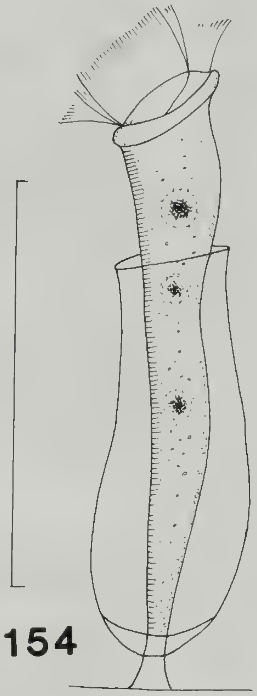

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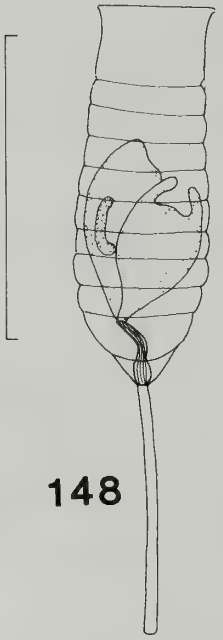

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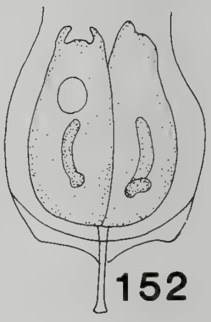

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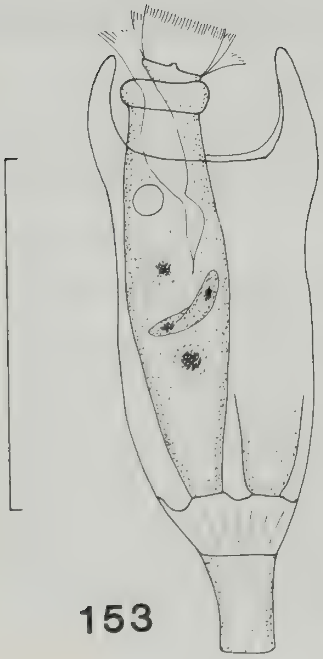

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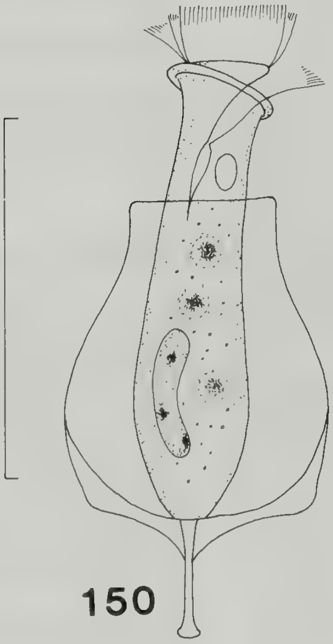

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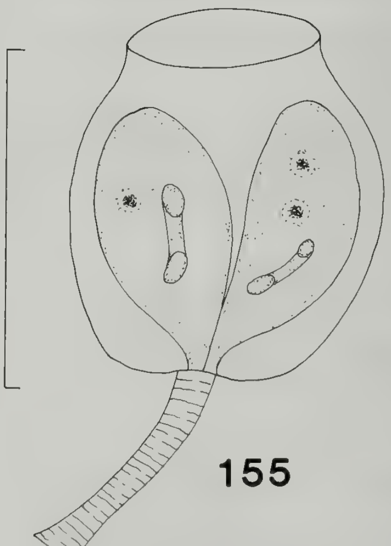

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Cothurnia recurvata Kahl, 1928

DESCRIPTION (Fig. 147). Lorica 100 μm long × 50 μm wide. Aperture 30 μm in diameter with curved neck. External stalk slender, 25 μm long attached to substratum via basal disc, 15 μm in diameter; endostyle short and broad; mesostyle absent. Zooid 75 μm long × 40 μm wide when contracted.

HABITAT. Brackish water, originally found attached to algae (Kahl, 1928).

NOTE. *C. recurvata* is very similar to *C. recurva*, the principal differences being those of size, host and habitat. It is possible that re-examination will show these taxa to be synonymous.

Cothurnia rhabdota Bock, 1952

Sincothurnia rhabdota (Bock, 1952) Jankowski, 1985

DESCRIPTION (Fig. 148). Lorica cylindrical, 125–130 μm × 40–42 μm wide with several (about eight) annular furrows. External stalk 88–93 μm long; mesostyle short; endostyle 20–22 μm long. Mesostyle and endostyle with continuous longitudinal striae. Two zooids per lorica, each 55 μm long × 28 μm wide when contracted. Macronucleus short, C-shaped and lies longitudinally in centre of zooid.

HABITAT. Marine, originally found attached to the red alga *Polysiphonia nigrescens* (Bock, 1952).

NOTE. Uncontracted specimens of this species have yet to be described.

Cothurnia richtersi (Penard, 1914) Kahl, 1935

Cothurniopsis richtersi Penard, 1914

DESCRIPTION (Figs 150–152). Lorica 45–60 μm long × 30–35 μm wide, rounded posteriorly. Aperture oval when viewed from above, 25 μm × 13 μm. External stalk slender, 20 μm long; mesostyle short and slender; endostyle absent. Two zooids per lorica, each 80 μm long × 20 μm wide, extending up to one third of its length beyond aperture. Peristomial lip 20 μm in diameter. CV situated near mid-region of infundibulum which reaches about one third zooid length. Macronucleus 20 μm long and lies either longitudinally or horizontally in posterior part of zooid. Pellicular striations inconspicuous.

HABITAT. Freshwater, reported by Penard (1914) from both France and Antarctic regions.

NOTE. If coloniality (*sensu* Jankowski, 1985) is accepted as a generic character, this species should be included in the genus *Sincothurnia*.

Cothurnia ruthae Lüpkes, 1974

DESCRIPTION (Fig. 149). Lorica conical in shape, 66 μm long × 30 μm wide, posterior end flattened and broad. Aperture 12 μm in diameter. External stalk slender, 27 μm long; mesostyle short; endostyle absent. Two zooids per lorica, each 93 μm long × 12 μm wide with annular constriction near posterior end. Peristomial lip 10 μm in diameter. Disc obliquely raised above peristome. Macronucleus irregular and lies longitudinally in posterior half of zooid. Pellicle with fine striations.

HABITAT. Freshwater, originally isolated from interstitial groundwater from the Fulda Valley (Lüpkes, 1974).

Cothurnia sieboldii Stein, 1854

DESCRIPTION (Fig. 153). Lorica 113–132 μm long × 30–49 μm wide with two horn-like processes projecting up and backwards on either side of aperture. External stalk and mesostyle both short and broad; endostyle absent. Two zooids per lorica, each 130 μm long × 30 μm wide. Peristomial lip well developed, 30 μm in diameter. Infundibulum broad, almost reaching centre of zooid. CV situated about one third of way down zooid. Macronucleus short, curved or U-shaped, and lies in centre of zooid.

HABITAT. Freshwater, found on *Entomostraca* (Kahl, 1935) and also on the crayfish *Astacus fluviatilis* and *A. torrentium* (Matthes and Guhl, 1973).

NOTE. If coloniality (*sensu* Jankowski, 1985) is accepted as a generic character, this species should be included in the genus *Sincothurnia*.

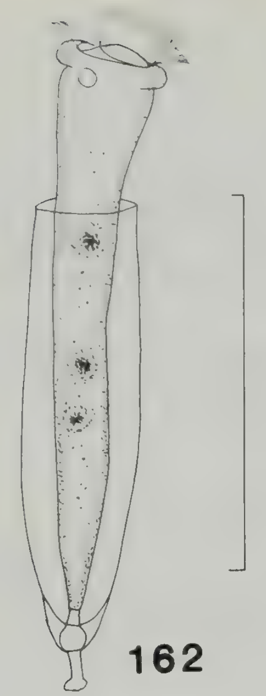
Cothurnia simplex Kahl, 1933

DESCRIPTION (Fig. 154). Lorica 50–60 μm long × 23 μm wide. Aperture 18 μm in diameter. External stalk short and broad with longitudinal striae; mesostyle and endostyle short and inconspicuous. Zooid 90 μm long × 15 μm wide, extending up to one quarter of its length beyond aperture. Peristomial lip 20 μm in diameter. CV situated just below peristome. Macronucleus vermiform and irregularly coiled. Pellicle with fine striations.

HABITAT. Marine, originally found attached to algae at Helgoland (Kahl, 1933), and at Plymouth (Felinska, 1965).

NOTE. *C. simplex* was redescribed by Felinska (1965).

Fig. 143 *Cothurnia propinqua*, after Kahl, 1933, bar = 50 μm.
Fig. 144 *Cothurnia pupa*, after Kent, 1881 (dimensions not available).
Figs 145 & 146 *Cothurnia recurva*; fig. 145 after Felinska, 1965, bar = 50 μm; fig. 146 after Claparede and Lachmann, 1858.
Fig. 147 *Cothurnia recurvata*, after Kahl, 1935, bar = 100 μm.
Fig. 148 *Cothurnia rhabdota*, after Bock, 1952, bar = 100 μm.
Fig. 149 *Cothurnia ruthae*, after Lüpkes, 1974, bar = 50 μm.
Figs 150–152 *Cothurnia richtersi*, after Penard, 1914; fig. 150 bar = 50 μm; fig. 151 nuclei; fig. 152 lorica with two contracted zooids.
Fig. 153 *Cothurnia sieboldii*, after Matthes and Guhl, 1973, bar = 100 μm.
Fig. 154 *Cothurnia simplex*, after Kahl, 1933, bar = 50 μm.
Fig. 155 *Cothurnia subglobosa*, after Daday, 1911, bar = 50 μm.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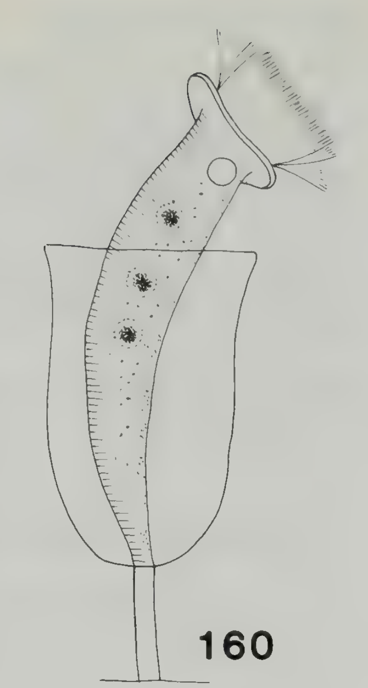
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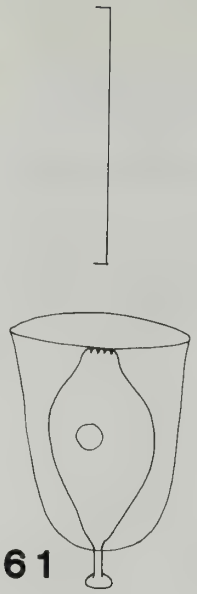
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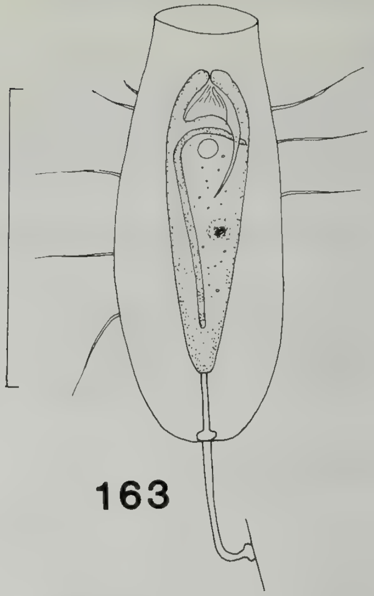
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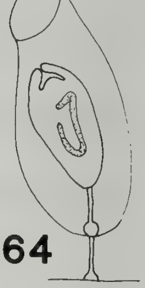
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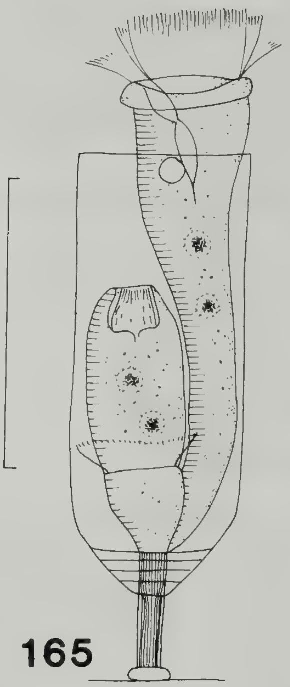
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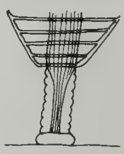
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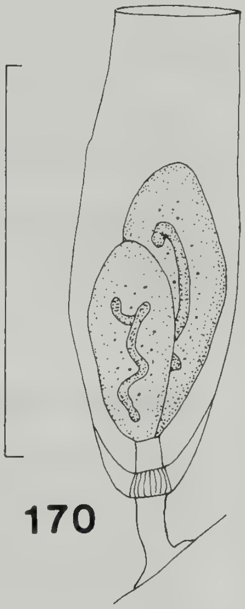
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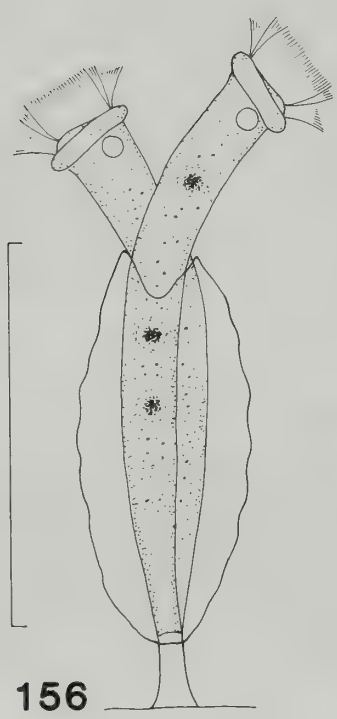
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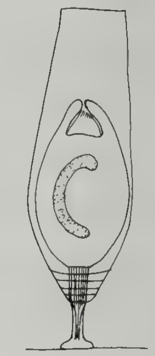
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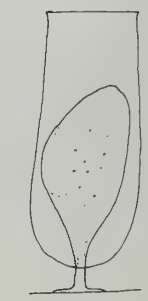
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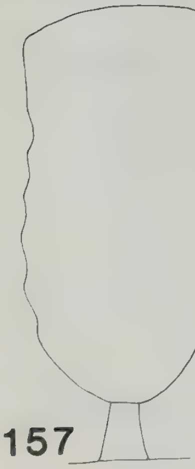
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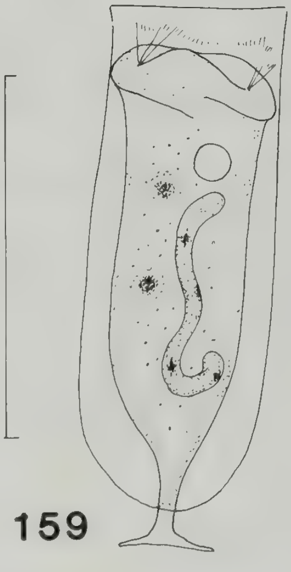
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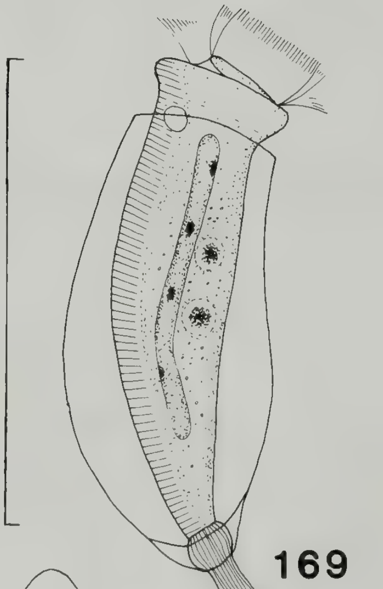
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Cothurnia sinuosa (Wailes, 1943) n. comb.

Cothurnia compressa? Kahl, 1935
Cothurnia compressa var. *sinuosa* Wailes, 1943
Sincothurnia sinuosa (Wailes, 1943) Jankowski, 1985

DESCRIPTION (Figs 156 & 157). Lorica compressed dorso-ventrally, 90–100 μm long × 35–40 μm long, tapering at both ends and with annular ridges. Aperture 40 μm × 15 μm with two deep clefts. External stalk 10 μm long; endostyle short and inconspicuous; mesostyle absent. Two zooids per lorica, each 150 μm long × 15 μm wide and extending up to one third of its length beyond aperture. Peristomial lip 25 μm in diameter. Pellicular striations inconspicuous.

HABITAT. Marine, originally found attached to algae from North America (Wailes, 1943).

Cothurnia soldida Vuxanovici, 1962

DESCRIPTION (Figs 158 & 159). Lorica 68 μm × 30 μm wide, cylindrical and rounded posteriorly. Aperture 30 μm in diameter. External stalk short; mesostyle and endostyle absent. Zooid 65 μm long × 20 μm wide, not reaching as far as aperture. CV situated near anterior end of macronucleus which is vermiform and curved at both ends. Pellicular striations inconspicuous.

HABITAT. Freshwater, originally found on decomposed plant material from Lake Fundeni, Bucharest (Vuxanovici, 1962).

Cothurnia spissa Fromentel, 1874

Cothurnia calix (Wailes, 1928) Kahl, 1933

DESCRIPTION (Figs 160 & 161). Lorica inverted bell-shaped, 60 μm long × 30–35 μm wide and rounded posteriorly. Aperture 36 μm in diameter. External stalk 10–12 μm long and slender; mesostyle and endostyle absent. Zooid 40 μm long × 15 μm wide when contracted. CV centrally located. Pellicle clearly striated.

HABITAT. Freshwater, originally found attached to *Confervae* (Fromentel. 1874).

NOTE. *C. calix* (Wailes, 1928) Kahl, 1933 shows only minor differences from *C. spissa* with which it is here synonymised.

Cothurnia stylarioides Precht, 1935

DESCRIPTION (Fig. 162). Lorica cylindrical, 121 μm long × 32 μm wide. Aperture 30 μm in diameter. External stalk 12 μm long and slender; mesostyle short and broad; endostyle inconspicuous. Zooid elongate, 145 μm long × 20 μm in diameter, extending up to one third of its length beyond aperture. Peristomial lip 30 μm in diameter. CV situated just beneath peristome. Pellicular striations inconspicuous.

HABITAT. Marine, originally found as an epizoite of the polychaete *Stylarioides plumosus* (Precht, 1935).

Cothurnia subglobosa (Daday, 1911) n. comb.

Cothurniopsis subglobosa Daday, 1911

DESCRIPTION (Fig. 155). Lorica ovoid, 45–50 μm long × 46–52 μm wide. Aperture 28–34 μm in diameter. External stalk 35–37 μm long; mesostyle and endostyle absent. Two zooids per lorica. Macronucleus C-shaped and lies longitudinally in centre of zooid.

HABITAT. Marine, originally isolated from the Antarctic region as an epizoite of the ostracod *Cythereis* (Daday, 1911).

NOTE. With the submergence of the genus *Cothurniopsis* by Kahl (1935), this species was transferred to *Cothurnia*. If, however, coloniality (*sensu* Jankowski, 1985) is accepted as a generic character, this species should be included in the genus *Sincothurnia*.

Cothurnia subtilis Stiller, 1939

DESCRIPTION (Figs 163 & 164). Lorica 65–72 μm long × 28 μm wide. Aperture 20 μm in diameter. External stalk 25–30 μm long; endostyle 10–15 μm long and slightly swollen at distal end; mesostyle absent. Contracted zooid 50 μm long × 15 μm wide. Macronucleus J-shaped. Pellicular striations inconspicuous.

HABITAT. Marine, originally found attached to *Mytilus edulis* (Stiller, 1939).

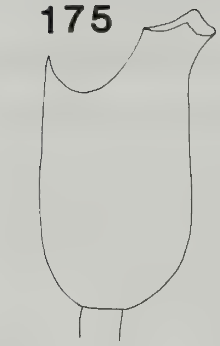
NOTE. Uncontracted specimens of this species have yet to be described.

Cothurnia tekirghiolica Tucolesco, 1962

DESCRIPTION (Figs 165–167). Lorica 80 μm long × 30 μm wide. Aperture oval when viewed from above, 30 μm × 20 μm. External stalk 15 μm long with irregular ridges and furrows; mesostyle short; endostyle short and inconspicuous. All three stalks with continuous longitudinal striae. Zooid 80 μm long × 20 μm wide, extending up to one third of its length beyond aperture. Peristomial lip well developed, 25 μm in diameter. CV situated near base of infundibulum. Macronucleus C-shaped and lies longitudinally in the centre of zooid. Pellicle clearly striated.

HABITAT. Freshwater, originally found attached to *Cladophora* from Lake Tekirghiol (Tucolesco, 1962).

Figs 156 & 157 *Cothurnia sinuosa*, after Wailes, 1943, bar = 100 μm.
Figs 158 & 159 *Cothurnia soldida*, after Vuxanovici, 1962, bar = 50 μm.
Figs 160 & 161 *Cothurnia spissa*; fig. 160 after Kahl, 1933, bar = 50 μm (called *Cothurnia calix*); fig. 161 after Fromentel, 1874.
Fig. 162 *Cothurnia stylarioides*, after Precht, 1935, bar = 100 μm.
Figs 163 & 164 *Cothurnia subtilis*, after Stiller, 1939, bar = 50 μm.
Figs 165–167 *Cothurnia tekirghiolica*, after Tucolesco, 1962; fig. 165 with developing telotroch, bar = 50 μm; fig. 166 external stalk and endostyle; fig. 167 contracted zooid.
Figs 168 & 169 *Cothurnia triangula*, after Precht, 1935; fig. 168 aperture, anterior view; fig. 169 bar = 50 μm.
Fig. 170 *Cothurnia trophoniae*, composite after Dons, 1946, bar = 100 μm.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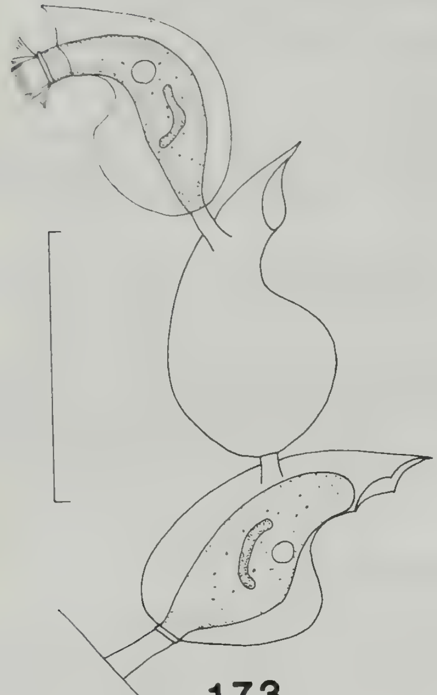
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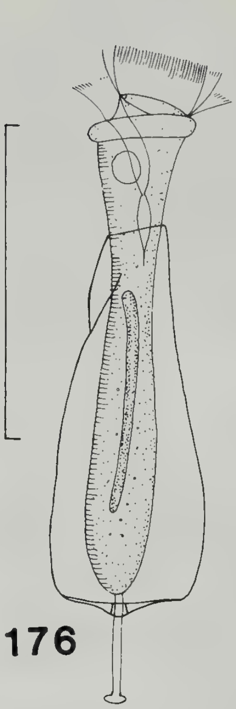
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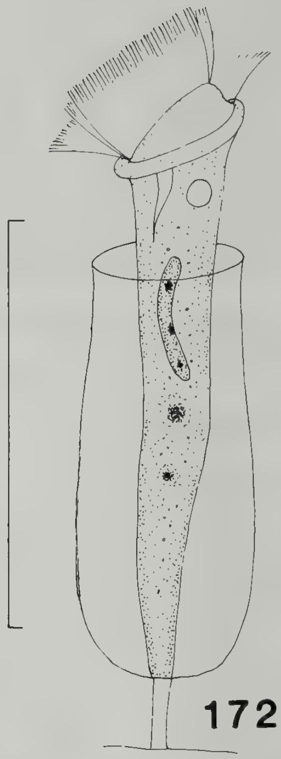
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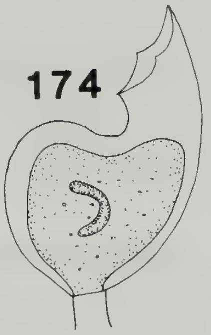
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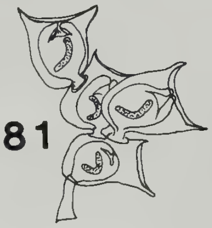
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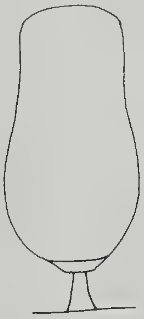
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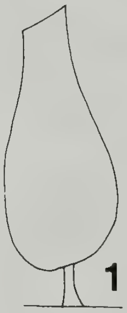
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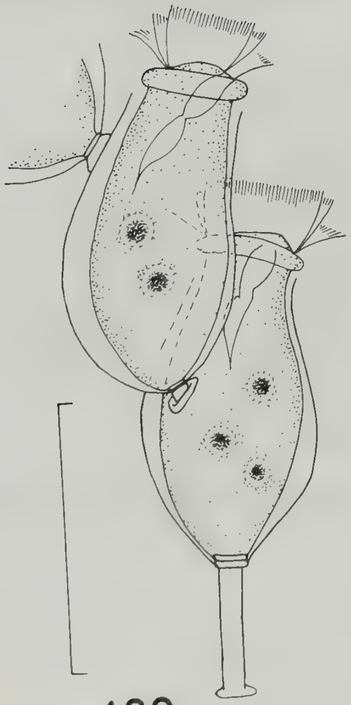
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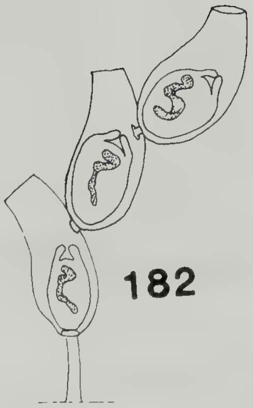
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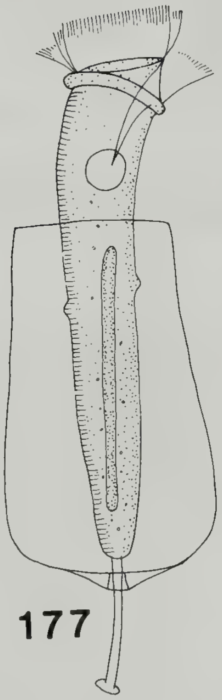
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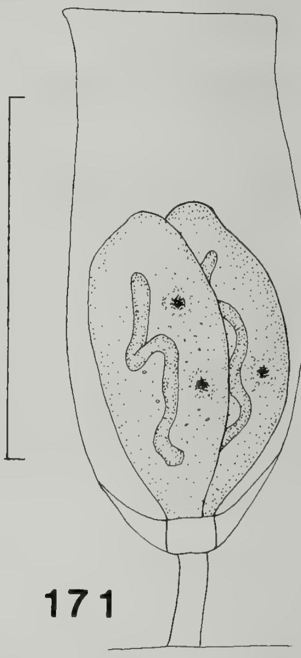
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Cothurnia triangula Precht, 1935

DESCRIPTION (Figs 168 & 169). Lorica curved, 45 μm long × 18 μm wide. Aperture triangular when viewed from above, 14 μm across. External stalk curved, 10–15 μm long; mesostyle short and broad; endostyle short and inconspicuous. All three stalks with conspicuous longitudinal striae. Zooid 40–45 μm long × 12 μm wide, extending just beyond aperture. Peristomial lip well developed, 14 μm in diameter. CV situated near anterior end of macronucleus which is 27 μm long and lies longitudinally in zooid. Pellicle clearly striated.

HABITAT. Marine, originally found as an epibiont of the halacarid *Copidognathus fabriciusi* and the ostracod *Cythereis tuberculata* (Precht, 1935).

Cothurnia trophoniae Dons, 1946

Cothurnia pedunculata Dons, 1918
Cothurnia nodosa Mereschkowsky, 1879 (in part) Dons, 1918

DESCRIPTION (Fig. 170). Lorica roughly cylindrical, 125–140 μm long × 40–50 μm wide. External stalk 65–135 μm long; mesostyle short and broad with conspicuous longitudinal striae; endostyle short. Two zooids per lorica, each 70 μm long × 35 μm wide when contracted. Macronucleus vermiform and coiled irregularly. Pellicular striations inconspicuous.

HABITAT. Marine, found as an epibiont of the alga *Polysiphonia violacea* (Dons, 1918), the polychaetes *Trophonia plumosa* and *Stylarioides plumosus* (Dons, 1946; Precht, 1935), the cnidarian *Laomedea loveni* and the pantopod *Pallene brevirostris* (Precht, 1935).

NOTE. Dons (1946) applied the name *C. trophoniae* to *C. nodosa* Mereschkowsky, 1879, an organism which Dons (1918) had previously redescribed under the name *C. pedunculata*. It is unclear why Dons (1946) chose not to use the name *C. pedunculata* for this species as it would appear to have priority over the name *C. trophoniae*. Furthermore, if coloniality (*sensu* Jankowski, 1985) is accepted as a generic character, this species should be included in the genus *Sincothurnia*. *C. trophoniae* was redescribed by Precht (1935).

Cothurnia trophonicola Dons, 1946

DESCRIPTION (Fig. 171). Lorica irregular and variable in shape, 60–85 μm long × 31–35 μm wide. Aperture oval when viewed from above, 12–16 μm × 30–33 μm. External stalk 5–15 μm long × 3–4 μm wide; mesostyle 4–6 μm long × 6–8 μm wide; endostyle absent. Two zooids per lorica, each 50 μm long × 25 μm wide when contracted. Macronucleus vermiform and coiled irregularly. Pellicular striations inconspicuous.

HABITAT. Marine, originally found as an epizoite of the polychaete *Trophonia plumosa* (Dons, 1946).

NOTE. If coloniality (*sensu* Jankowski, 1985) is accepted as a generic character, this species should be included in the genus *Sincothurnia*.

Cothurnia vaga Roux, 1901

DESCRIPTION (Fig. 172). Lorica cylindrical, 100 μm long × 45 μm wide and rounded posteriorly. External stalk short and slender; mesostyle and endostyle absent. Zooid 140 μm long × 30 μm wide, extending up to one third of its length beyond aperture. Peristomial lip 45 μm in diameter. CV situated beneath peristome. Macronucleus short, curved and lies in centre of zooid. Pellicular striations inconspicuous.

HABITAT. Freshwater, originally found as an epizoite of the crustaceans *Cyclops* and *Gammarus* (Roux, 1901).

Cothurnia variabilis Kellicott, 1883

Cothurnia variabilis var. *emarginata* (Kellicott, 1883a) Stokes, 1888
Daurotheca variabilis (Kellicott, 1883) Jankowski, 1987
Daurotheca marginata (Kellicott, 1883) Jankowski, 1987

DESCRIPTION (Figs 173–175). Lorica 75–130 μm long, variable in shape but usually rounded posteriorly and with curved neck. One or more spines may be present either near aperture or at posterior end of lorica. Aperture 30–40 μm wide. External stalk short and broad; mesostyle and endostyle absent. May form pseudocolonies with several loricas attached to each other via their external stalks to form chains. Two zooids per lorica, each 75–130 μm long × 25–45 μm wide and extending just beyond aperture. Diameter of peristomial lip slightly less than maximum body width. Infundibulum broad and reaches one third of zooid length. CV situated near centre of zooid. Macronucleus C-shaped and lies either in centre or in lower half of zooid. Pellicular striations inconspicuous.

HABITAT. Freshwater, found as an epizoite of the crayfish *Cambarus diffinis*, *C. propinquus*, *C. bartonii*, *C. affinis*, *Astacus leptodactylus* and *A. fluviatilis* (Kellicott, 1883a; Nenninger, 1948; Krucinska and Simon, 1968).

NOTE. Jankowski (1987) transferred this species and *C. variabilis* var. *emarginata* Kellicott, 1883 (as *Daurotheca marginata*) to *Daurotheca*. However, since *Daurotheca* is of uncertain taxonomic status (see Incertae Sedis), *C. variabilis* is retained in the genus *Cothurnia*.

Genus ***COTHURNIOPSIS*** Stokes, 1893

The genus *Cothurniopsis* was erected by Stokes (1893) for peritrichs which resemble *Cothurnia* in every respect save

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Fig. 171 *Cothurnia trophonicola*, after Dons, 1946, bar = 50 μm.
Fig. 172 *Cothurnia vaga*, after Roux, 1901, bar = 100 μm.
Figs 173–175 *Cothurnia variabilis*; fig. 173 chain of individuals forming a pseudocolony, bar = 100 μm; figs 174 & 175 after Kellicott, 1883 (fig. 175—called *Cothurnia variabilis* var. *emarginata*).
Figs 176–179 *Cothurniopsis valvata*; figs 176 & 177 composite after Penard, 1914, bar = 50 μm (called *Cothurniopsis elastica*); figs 178 & 179 composite after Stokes, 1893.
Figs 180–182 *Dimorphocothurnia nebaliae*; figs 180 & 181 after Jankowski, 1985, bar = 100 μm; fig. 182, after Dons, 1928.

one, that is the lateral borders of the lorica are pliable and are used to close the aperture when the ciliate contracts. By contrast *Cothurnia* has no mechanism of closing its aperture.

The name *Cothurniopsis* has, on several occasions, been erroneously confused with Entz's (1884) genus *Cothurnopsis*. According to Entz (1884) the principal characters by which *Cothurnopsis* is distinguished from *Cothurnia* are the possession of, (i) a large, transversely folded external stalk, and (ii) a compact macronucleus. Like *Cothurnia*, *Cothurnopsis* has no mechanism for closing its aperture. Unfortunately the similarity of the two names *Cothurniopsis* and *Cothurnopsis* has led to some confusion. For example Penard (1914), Zelinka (1928) and Kahl (1935) have either transferred existing species or described new species using the generic name *Cothurniopsis*. Yet in almost every case, the organisms concerned conformed to *Cothurnopsis* (*sensu* Entz, 1884) rather than *Cothurniopsis* (*sensu* Stokes, 1893). Jankowski (1985) cites other examples of such errors.

Stokes (1893) described a single species of *Cothurniopsis*, *C. valvata*, which became the type species by monotypy. *Cothurniopsis elastica* Penard, 1914 is the only cothurnid described since which possesses a closeable aperture.

Diagnosis of *Cothurniopsis*

Lorica erect and borne upon a stalk. Aperture border pliable and closes aperture when zooid contracts.

Key to the species of *Cothurniopsis*

1 Anterior lateral borders pliable and close aperture upon contraction of zooid(s) .... *C. valvata*

Species description

Cothurniopsis valvata Stokes, 1893

Cothurnia elastica (Penard, 1914) Kahl, 1935
Cothurnia valvata (Stokes, 1893) Kahl, 1935
Cothurniopsis elastica Penard, 1914

DESCRIPTION (Figs 176–179). Lorica 50–70 μm long × 25–35 μm wide and rounded posteriorly. Aperture oval when viewed from above, 20 μm long × 10 μm wide. External stalk 10–18 μm long. Zooid 75–80 μm long × 10–15 μm wide, extending up to one third of its length beyond aperture. CV situated in anterior half of body. Macronucleus straight and lies longitudinally in posterior half of body. Pellicle with fine striations.

HABITAT. Brackish or freshwater, originally found attached to filamentous algae from Coney Island, New York, USA (Stokes, 1893); also isolated from moss in Europe (Penard, 1914).

NOTE. Penard (1914) described several species under the generic name *Cothurniopsis* although only one, *C. elastica*, has pliable lateral borders enabling the aperture to be closed. *C. elastica* shows only minor differences from *C. valvata* so the two are synonymised.

Genus *CYCLODONTA* Matthes, 1958

The genus *Cyclodonta* was erected by Matthes (1958) for *Cothurnia bipartita* Stokes, 1885, which differs from other species of *Cothurnia* in that the zooid is attached to the inside of the lorica via a series of membranes rather than via an endostyle or mesostyle. In all other respects, *Cyclodonta* resembles *Cothurnia*. *C. bipartita* is the only species of *Cyclodonta* and so becomes the type species by monotypy.

Cyclodonta is commonly included in the family Vaginicolidae (Corliss, 1979; Foissner, 1979), although according to Stiller (1971) it should belong to the family Lagenophrydae because of its mode of development.

Diagnosis of *Cyclodonta*

Lorica borne upon a short stalk and without valves or other means of closing aperture. Zooid attached to lorica via a series of membranes. Mesostyle and endostyle absent. Single species genus.

Key to the species of *Cyclodonta*

1 Zooid attached to the lorica via a series of membranes .... *C. bipartita*

Species description

Cyclodonta bipartita (Stokes, 1885) Matthes, 1958

Cothurnia affinis (Kahl, 1935) Matthes, 1958
Cothurnia bipartita Stokes, 1885
Cothurniopsis rheotypica (Stiller, 1931) Felinska, 1965
Cothurnia trilobata (Sramek-Husek, 1957) Matthes, 1958
Cothurnia voigti (Voigt, 1902) Kahl, 1935
Cothurniopsis longipes Voigt, 1902

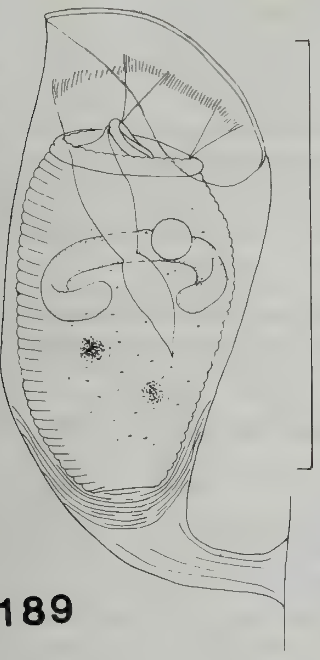
DESCRIPTION (Figs 183–189). Lorica curved, 78–132 μm long × 40–70 μm wide with fine, longitudinal striae. Aperture 40–70 μm in diameter. External stalk curved, 20 μm long, with transverse furrows. 2–6 membranes present at posterior end of lorica; mesostyle and endostyle absent. Zooid 40–105 μm long × 29–62 μm wide, not extending as far as aperture. CV empties into infundibulum via short channel. Macronucleus variable in shape, from short and curved to vermiform. Pellicle clearly striated with convex ribbing between striations.

HABITAT. Freshwater, commonly found attached to harpacticoid copepods (Matthes, 1958; Jankowski, 1985); also found attached to the crayfish *Cambarus affinis* and *Astacus leptodactylus* (Krucinska and Simon, 1968).

NOTE. *Cyclodonta bipartita* has been isolated by several workers including Voigt (1902), Penard (1914), Kahl (1935), Matthes (1958) and Foissner (1979), and in every case the host was a freshwater harpacticoid copepod. Indeed Jankowski (1985) has suggested that the absence of *Cothurnia* from these hosts is due to its substitution by *Cyclodonta*. However, *Cyclodonta* does not appear to be confined exclusively to harpacticoid copepod hosts as suggested by Jankowski (1985), since it has also been isolated (as *Cothurnia bipartita*) from the crayfish *Cambarus affinis* and *Astacus leptodactylus* (Krucinska and Simon, 1968).

Genus *DIMORPHOCOTHURNIA* Jankowski, 1980

The genus *Dimorphocothurnia* was first mentioned by Jankowski (1980), although a full generic description did not appear until five years later (Jankowski, 1985). *Dimorpho-*



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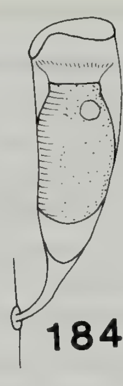

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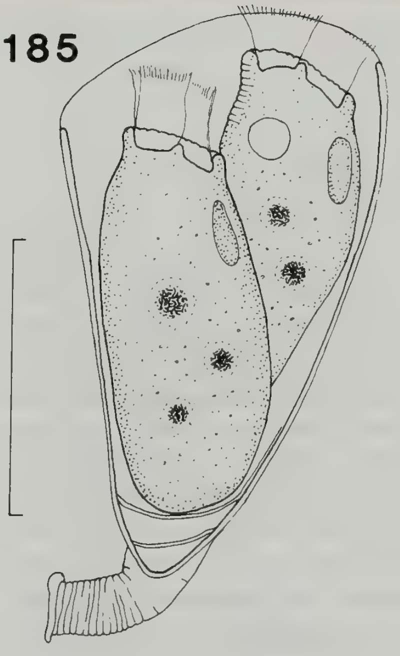

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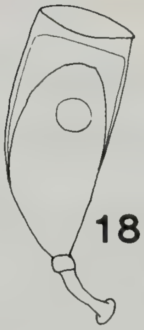

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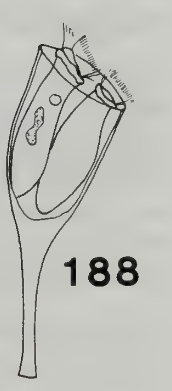

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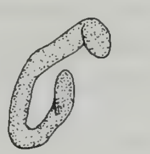

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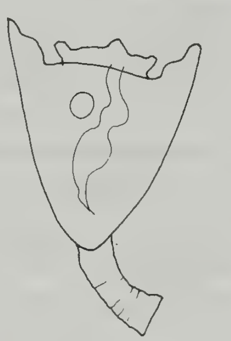

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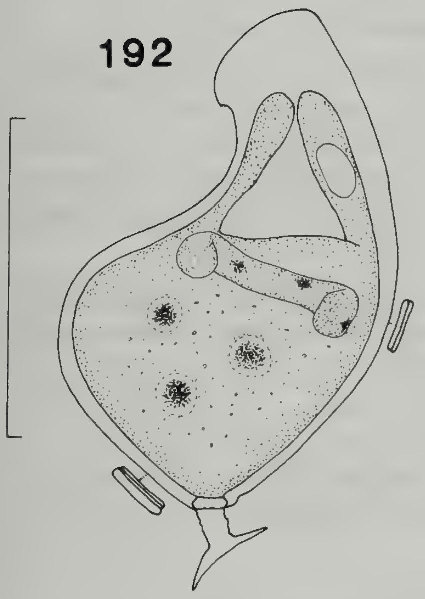

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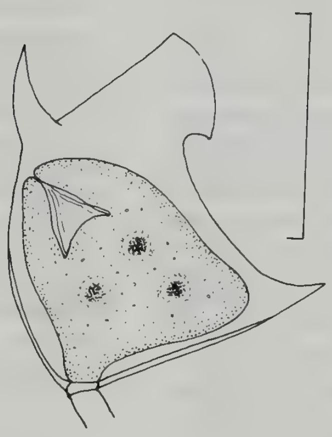

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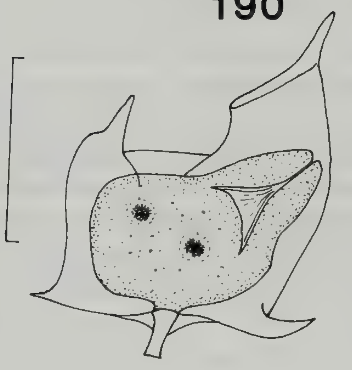

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Figs 183–189 *Cyclodonta bipartita*; fig. 183 after Sramek-Husek, 1957 (called *Cothurnia trilobata*); fig. 184 after Stokes, 1885; figs 185 & 186 after Matthes, 1958 (fig. 185 bar = 50 μm; fig. 186 macronucleus); fig. 187 after Voigt, 1902 (called *Cothurnia longipes*); fig. 188 after Stiller, 1931 (called *Cothurniopsis rheotypica*); fig. 189 after Foissner, 1979, bar = 50 μm.
Fig. 190 *Daurotheca tespa*, after Jankowski, 1987, bar = 50 μm.
Fig. 191 *Daurotheca transoceanica*, after Jankowski, 1987, bar = 50 μm.
Fig. 192 *Daurotheca ussurina*, after Jankowski, 1987, bar = 50 μm.

cothurnia was erected for *Cothurnia nebaliae* Dons, 1928 which typically forms pseudocolonies with several individuals attached to each other via their external stalks to form chains. Although other species of *Cothurnia*, e.g. *C. bavarica* and *C. variabilis*, also form pseudocolonies they differ from *Dimorphocothurnia* in one important respect; that is, in *C. bavarica* and *C. variabilis* all the individual loricas of any chain are identical, whereas *Dimorphocothurnia* exhibits lorica dimorphism with the individual in contact with the substratum ('basont' Jankowski, 1985) having a longer stalk than those of the rest of the chain. *D. nebaliae* is the only species of *Dimorphocothurnia* and is the type species by monotypy.

Diagnosis of *Dimorphocothurnia*

Lorica without valves or any other means of closing aperture. Forms pseudocolonies with several loricas joined together via their external stalks to form chains. Exhibits lorica dimorphism with lorica in contact with substratum ('basont') having longer external stalk than those in rest of chain. Single species genus.

Key to the species of *Dimorphocothurnia*

1 Forms pseudocolonies and exhibits lorica dimorphism

with individual in contact with substratum having longer external stalk than others in chain .... ***D. nebaliae***

Species description

Dimorphocothurnia nebaliae (Dons, 1928) Jankowski, 1985

Cothurnia nebaliae Dons, 1928

DESCRIPTION (Figs 180–182). Lorica 100–120 μm long × 40–55 μm wide. Aperture 20–35 μm in diameter. Forms pseudocolonies with several loricas joined together via their external stalks to form chains. External stalk of individual in contact with substratum ('basont'), 30–40 μm long × 6–7 μm wide; those of rest of chain, 5 μm long × 6–7 μm wide. Mesostyle short and broad; endostyle absent. Zooid 140 μm long × 60 μm wide and extends just beyond aperture. Peristomial lip well developed, 50 μm in diameter. Disc convex. Macronucleus vermiform, 40–50 μm long and irregularly coiled. Pellicular striations inconspicuous.

HABITAT. Marine, originally isolated from Norwegian coastal waters attached to the phyllocarid *Nebalia bipes* (Dons, 1928); also isolated from phyllocarids by Jankowski (1980, 1985).

INCERTAE SEDIS

Genus *DAUROTHECA* Jankowski, 1987

The genus *Daurotheca* was erected by Jankowski (1987) for cothurnids which have asymmetrical loricas and zooids, and exhibit a tendency to form spines on their loricas. Neither feature has previously been used for separating peritrich genera, and data on their reliability as taxonomic characters is scarce. In all other respects *Daurotheca* resembles *Cothurnia*.

Two cothurnids, *Cothurnia variabilis* Kellicott, 1883 and *C. variabilis* var. *emarginata* Kellicott, 1883 were transferred by Jankowski (1987) to *Daurotheca*. However, until the taxonomic status of *Daurotheca* has been established these taxa should remain in the genus *Cothurnia*. Jankowski (1987) also described three new species, *Daurotheca transoceanica*, *D. tespa* and *D. ussurina*.

Diagnosis of *Daurotheca*

Lorica asymmetrical, often with spines. Attached to substratum via external stalk. Aperture narrow, inclined at oblique angle to main lorica axis. Neck short. Zooid asymmetrical and bends to one side upon contraction.

Key to the species of *Daurotheca*

1 Lorica with spines 2
Lorica without spines .... ***D. ussurina***

2 Lorica with two spines, one subapical, one basal .... ***D. transoceanica***
Lorica with four spines, one apical, one subapical and two basal .... ***D. tespa***

Species descriptions

Daurotheca tespa Jankowski, 1987

DESCRIPTION (Fig. 190). Lorica trapezoid, 86–92 μm long × 58–64 μm wide and with four spines, one broad apical (20 μm long), one slender subapical (14 μm long), and two basal (8 μm long). Apical and subapical spines point upwards, basal spines horizontally. Aperture held at angle to main lorica axis on short, broad neck. External stalk short; mesostyle and endostyle absent.

HABITAT. Freshwater, originally found attached to the gills of the crustacean *Pacifastacus lenisculus* (Jankowski, 1987).

Daurotheca transoceanica Jankowski, 1987

DESCRIPTION (Fig. 191). Lorica roughly triangular, 69–74 μm long × 60–75 μm wide. Anterior region constricted to form a neck. Dorsal side of neck straight, 29–33 μm long. Aperture 22–25 μm wide. Lorica with two spines, one subapical 21 μm long, the other basal 10 μm long. External stalk up to 8 μm long; mesostyle short and inconspicuous; endostyle absent. Zooid 45 μm long × 45 μm wide when contracted.

HABITAT. Freshwater, originally found attached to the crustacean *Pacifastacus lenisculus* (Jankowski, 1987).

Daurotheca ussurina Jankowski, 1987

DESCRIPTION (Fig. 192). Lorica somewhat rotund, 69–74 μm long × 42–46 μm wide. Aperture 20–23 μm wide. Neck narrow. External stalk 7–8 μm long × 3 μm wide; mesostyle short and broad; endostyle absent. Zooid 65 μm long × 45 μm wide when contracted. Macronucleus C-shaped and lies horizontally in anterior part of zooid.

HABITAT. Freshwater, originally found attached to the crustaceans *Cambaroides*, *Cambarus*, *Orconectes* and *Pacifastacus* (Jankowski, 1987).

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INDEX TO SPECIES

The following is an annotated list of nominal species as well as an index of extant species.

Cothurnia

C. acuta Wang & Nie, 1933 = *Vaginicola wangi* (Wang & Nie, 1933) Kahl, 1935.

C. acuta Levander, 1915 (p. 26).

C. affinis Blochmann, 1886 = *Pyxicola pusilla* Wrzesniowsky, 1866) Trueba, 1978.

C. affinis Kahl, 1935 = *Cyclodonta bipartita* (Kahl, 1935) Matthes, 1958

C. amoyensis Wang, 1935 (p. 26).

C. amphicteis Lang, 1948 (p. 26).

C. amphora Kahl, 1928 = *Vaginicola amphora* Kahl (1928), 1935

C. amphorella Maskell, 1887 = *Vaginicola amphorella* (Maskell 1887) Kahl, 1935.

C. angusta Kahl, 1933 (p. 26).

C. annulata Stokes, 1885 (p. 26).

C. anomala Stiller, 1951 (p. 26).

C. antarctica (Daday, 1911) n. comb. (p. 27).

C. aplatita Stiller, 1939 (p. 27).

C. aplatita var. *flexa* Felinska, 1965 = *C. aplatita* n. comb.

C. apseudophila Lang, 1948 (p. 27).

C. arcuata Mereschkowsky, 1879 (p. 27).

C. arenata Kent, 1882 = *C. arcuata* (Kent, 1882) Zelinka, 1928.

C. asimmetrica Banina and Polyakova, 1977 (p. 27).

C. astaci Stein, 1854 (p. 27).

C. asymmetrica Sommer, 1951 (p. 27).

C. auriculata Stiller, 1939 (p. 29).

C. auriculata var. *flexa* Felinska, 1965 = *C. auriculata* n. comb.

C. bavarica Matthes & Guhl, 1973 (p. 29).

C. bipartita Stokes, 1885 = Cyclodonta bipartita (Stokes, 1885) Matthes 1958.

C. brevistyla Nenninger, 1948 (p. 29).

C. butschlii Zelinka, 1913 (p. 29).

C. calix (Wailes, 1928) Kahl, 1935 = *C. spissa* Fromentel, 1874 n. comb.

C. canthocampti Stokes, 1886 (p. 29).

C. carinogammari Stiller, 1953 (p. 29).

C. carteri Kent, 1881 = *Pyxicola constricta* Stokes, 1884 (Kahl, 1935).

C. castellensis Penard, 1914 = *Thuricola kellicottiana* (Stokes, 1887) Kahl, 1935.

C. ceramicola Kahl, 1933 (p. 29).

C. ceratophylli Penard, 1922 = *Vaginiola ceratophylli* (Penard, 1922) Kahl, 1935.

C. chaperoni Penard, 1922 = *Vaginicola chaperoni* (Penard, 1922) Kahl, 1935.

C. clausiens Stiller, 1951 (p. 31).

C. coarctata Kahl 1933 (p. 31).

C. cohni (Cohn, 1866) Kent, 1881 (p. 31).

C. collaris Kahl, 1933 (p. 31).

C. collaris var. *incisa* Felinska, 1965 = *C. collaris*.

C. complanata Precht, 1935 (p. 31).

C. compressa Claparede & Lachmann, 1858 (p. 33).

C. compressa var. *compressula* = *C. felinska* (Felinska, 1965) n. sp.

C. compressa var. *cyathiformis* Felinska, 1965 = *C. cyathiforme* Stiller, 1939.

C. compressa f. *flexa* Wailes, 1928 = *C. compressa*.

C. compressa var. *ovata* Dons, 1922 = Vaginicola ovata (Dons, 1922) Kahl, 1935.

C. compressa var. *sinuosa* Wailes, 1943 = *C. compressa*.

C. compressula (Wailes, 1928) Kahl, 1935 = *C. compressa*.

C. cordylophorae Kahl, 1933 (p. 33).

C. corrugata Davis, 1879 = *Pyxicola socialis* (Trueba, 1978).

C. cothurnoides Blochmann, 1886 = *Pyxicola pusilla* (Trueba, 1978).

C. cratera Swarczewsky, 1930 = *Vaginicola cratera* Kahl, 1935.

C. crystallina sensu Entz, 1884 = *Vaginicola crystallina* (Entz, 1884) Kahl, 1935.

C. crystallina sensu Entz, 1904 = *Pseudothuricola* dyonsii pro parte (Entz, 1904) Trueba, 1980, and *Thuricola kellicottiana pro parte* (Entz, 1904) Trueba, 1980.

C. crystallina sensu Penard, 1922 = *Thuricola gracilis* (Penard, 1922) Trueba, 1980.

C. curva Stein, 1867 (p. 33).

C. curvula Entz, 1884 (p. 33).

C. curvula sensu Dons, 1922 = *Vaginicola curvula* (Dons, 1922) Kahl, 1935.

C. cyathiforme Stiller, 1939 (p. 33).

C. cyathus Jaworowski, 1893 = *C. maritima* Ehrenberg, 1838.

C. cyclopis Kahl , 1933 (p. 33).

C. cylidrica Sommer, 1951 (p. 33).

C. cypridicola Kahl, 1933 (p. 35).

C. cytherideae Kahl, 1933 (p. 35).

C. doliola Stiller, 1939, was originally described as a provisional species ('sp. prov.') and has yet to be designated species status.

C. doliolum Penard, 1914 = *Vaginicola doliolum* (Penard, 1914) Kahl, 1935.

C. dubia Stiller, 1939 was originally described as a provisional species ('sp. prov.') and has yet to be designated species status.

C. elastica (Penard, 1914) Kahl, 1935 = *Cothurniopsis valvata* Stokes, 1893.

C. elegans Stiller, 1940 (p. 35).

C. elegans Swarczewsky, 1930 = *Vaginicola elegans* (Swarczewsky, 1930) Kahl, 1935.

C. elongata Felinska, 1965 (p. 35).

C. elongata Fromentel, 1876 = *Vaginicola elongata* (Fromentel, 1876) Kahl, 1935.

C. endostyla Jankowski. Although this species was mentioned by Jankowski (1985), no description of it could be located.

C. entzi Kahl, 1933 (p. 35).

C. fecunda Stokes, 1893 (p. 35).

C. felinska (Felinska, 1965) n. sp. (p. 35).

C. fibripes Kahl, 1933 (p. 36).

C. flexa Kahl, 1935 = *C. compressa* Claparede and Lachmann, 1858.

C. floscularia Perty, 1852 (p. 36).

C. furcifer Hutton, 1878 = *Pyxicola pusilla* (Hutton, 1878) Trueba, 1978.

C. fusiformis Gourret & Roeser, 1886 = *C. arcuata* (Zelinka, 1928).

C. gammari Precht, 1935 (p. 36).

C. gigantea d'Udekem, 1864 = *Vaginicola gigantea* (d'Udekem, 1864) Kahl, 1935.

C. globosa d'Udekem, 1864 = *Vaginicola globosa* (d'Udekem, 1864) Kahl, 1935.

C. gracilis Kent, 1881 = *C. curva*.

C. halacaricola Precht, 1935 (p. 36).

C. harpactici Kahl, 1933 (p. 36).

C. havniensis Ehrenberg, 1838 = *Acineta compressa* Claparede and Lachmann 1859 (Curds, 1985).

C. hofkeri Kahl, 1933 = *C. innata* Müller, 1786.

C. imberbis Ehrenberg, 1831 (p. 26).

C. imberbis var. *limbata* Stiller = *Pyxicola limbata* (Stiller) Kahl, 1935.

C. incisa Daday, 1907 = *Thuricola incisa* (Daday, 1907) Trueba, 1980.

C. inclinans Felinska, 1965 (p. 36).

C. inflata Stokes, 1893 (p. 37).

C. inflecta Stiller, 1939 (p. 37).

C. innata Müller, 1786 (p. 37).

C. irregularis Kent, 1881 (p. 37).

C. kahli Banina and Polyakova, 1977 (p. 37).

C. kellicottiana Stokes, 1887 = *Thuricola kellicottiana* (Stokes, 1887) Kahl, 1935.

C. lapponum Penard, 1922 (p. 38)

C. lapponum naidongensis = *C. lapponum* Wang Jiaji, 1977.

C. lata Kellicott, 1883 (p. 40).

C. lata (*sensu* Wailes, 1928) Kahl, 1935 = *C. lata* Kellicott, 1883.

C. ligiae Cuénot, 1891 = *Pyxicola ligiae* (Cuénot, 1891) Kahl, 1935.

C. limnoriae Dons, 1928 (p. 40).

C. lobata Daday, 1907 = *Vaginicola lobata* (Daday, 1907) Kahl, 1935.

C. longipes Kellicott, 1894 (p. 40).

C. longipes (*sensu* Mereschkowsky, 1879) Kahl, 1935 = *C. longipes* Kellicott, 1894.

C. longipes sensu Voigt, 1902 = *Cyclodonta bipartita* (Stokes, 1885) Matthes, 1958.

C. macrodisca Stiller (p. 40).

C. magna Yunfen, 1980 (p. 40).

C. marina Andrussowa, 1886 = *C. maritima* Ehrenberg, 1838.

C. maritima Ehrenberg, 1838 (p. 40).

C. maritima sensu Möbius, 1888 = *C. mobiusi* (Möbius, 1888) Stiller, 1939.

C. membranoloricata Stiller, 1968 (p. 42).

C. minutissima (Penard, 1914) Kahl, 1935 (p. 42).

C. mobiusi (Möbius, 1888) Stiller, 1939 (p. 42).

C. mobiusi mihi (Möbius, 1888) Stiller, 1939 = *C. mobiusi*.

C. monoannulata Banina & Polyakova, 1977 (p. 42).

C. nebaliae Dons, 1928 = *Dimorphocothurnia nebaliae* (Dons, 1928) Jankowski, 1980.

C. nereicola Precht, 1935 (p. 42).

C. nitocrae Precht, 1935 (p. 42).

C. nodosa Claparede & Lachmann, 1858 (p. 44).

C. nodosa sensu Fromentel, 1874 = *C. irregularis* (Fromentel, 1874) Kent, 1881.

C. nodosa var. *longipes* Mereschkowsky, 1879 = *C. longipes* (Mereschkowsky, 1879) Kahl, 1935.

C. obliqua Bock, 1952 (p. 44).

C. oblonga Kahl, 1935 (p. 44).

C. operculigera Kent, 1869 = *Pyxicola operculigera* Kent (1869), 1881.

C. operculata Gruber, (1879), 1880 = *Thuricola valvata* (Gruber, 1879, 1880) Kahl, 1935.

C. ovalis (Wailes, 1928) Kahl, 1935 (p. 44).

C. ovata Fromentel, 1874 (p. 44).

C. oviformis Banina and Polyakova, 1977 (p. 44).

C. paguri André, 1910 = *Vaginicola paguri* (André 1910) Kahl, 1935.

C. parallela Maskell, 1887 = *Vaginicola parallela* (Maskell, 1887) Kahl, 1935.
C. parva Bock, 1952 (p. 45).
C. parvula Felinska, 1965 (p. 45).
C. patellae Hutton (1878), 1881 = *Mantoscyphidia patellae* (Hutton (1878), 1881) Jankowski, 1985.
C. patula Fromentel, 1874 (p. 45).
C. pedunculata Dons, 1918 = *C. trophoniae* Dons (1918), 1946.
C. peloscolicis Precht, 1935 (p. 45).
C. plachteri Matthes & Guhl, 1973 (p. 45).
C. plectostyla Stokes, 1885 (p. 45).
C. poculum (Wailes, 1928) Kahl, 1933 = *C. patula*.
C. pontica Mereschkowsky, 1881 = *Vaginicola pontica* (Mereschkowsky, 1881) Kahl, 1935.
C. propinqua Kahl, 1933 (p. 45).
C. pupa Eichwald, 1849 (p. 45).
C. pupa Cohn, 1866 = *C. cohni* (Cohn, 1866) Kent, 1881.
C. pusilla Wrzesniowski, 1870 = *Pyxicola pusilla* (Wrzesniowski, 1870) Kahl, 1935.
C. putanea Jaworowski, 1893 = *C. imberbis* Ehrenberg, 1831 (Kahl, 1935).
C. pyxidiformis d'Udekem, 1864 = *Pyxicola pyxidiformis* (d'Udekem, 1864) Trueba, 1978.
C. pyxidiformis var. *lacustris* Maggi, 1879 = *Pyxicola pyxidiformis* var. *lacustris* (Maggi, 1879) Trueba, 1978.
C. recurva Claparede & Lachmann, 1858 (p. 45).
C. recurvata Kahl, (p. 47).
C. regalis Penard, 1914 = *Thuricola valvata* Wright, 1858 (Trueba, 1980).
C. rhabdota Bock, 1952 (p. 47).
C. rheotypica Stiller, 1931 = *Cyclodonta bipartita* Matthes, 1958 (Felinska, 1965).
C. richtersi (Penard, 1914) Kahl, 1935 (p. 47).
C. ruthae Lüpkes, 1974 (p. 47).
C. sahrhagei (Sahrhage) Kahl, 1933 = *C. nodosa*.
C. sediculum Penard, 1914 = *Vaginicola sediculum* (Penard, 1914) Kahl, 1935.
C. sieboldii Stein, 1854 (p. 47).
C. simplex Kahl, 1933 (p. 47).
C. sinuata Kahl, 1933 = *C. minutissima*.
C. sinuosa (Wailes, 1943) n. comb. (p. 49).
C. socialis Gruber (1879), 1880 = *Pyxicola socialis* (Gruber 1879, 1880) Kent, 1881.
C. soldida Vuxanovici, 1962 (p. 49).
C. spinosa Labbé, 1895. Only a brief description of this species exists and it has never been figured. *C. spinosa* is therefore declared a *nomen nudun*.
C. spissa Fromentel, 1874 (p. 49).
C. striata Gourret & Roeser, 1886 = *Vaginicola striata* (Gourret & Roeser, 1886) Kahl, 1935.
C. stylarioides Precht, 1935 (p. 49).
C. subglobosa (Daday, 1911) n. comb. (p. 49).
C. subtilis Stiller, 1939 (p. 49).
C. sulcata Kahl, 1928 = *Vaginicola sulcata* Kahl (1928), 1935.
C. tekirghiolica Tucolesco, 1962 (p. 49).
C. terricola (Greeff, 1888) Penard, 1914 = *Vaginicola terricola* Greeff, 1888.
C. thuricolae Shubernetskii, 1978 = *Pyxicola thuricolae* (Shubernetskii, 1978) n. comb.
C. triangula Precht, 1935 (p. 51).
C. trilobata Sramek-Husek, 1957 = *Cyclodonta bipartita* Stokes, 1885 (Matthes, 1958).
C. trophoniae Dons (1918), 1946 (p. 51).
C. trophonicola Dons, 1946 (p. 51).
C. vaga Roux, 1901 (p. 51).
C. valvata (Stokes, 1893) Kahl, 1935 = *Cothurniopsis valvata* Stokes, 1893.
C. valvata Dons, 1922 = *Thuricola valvata* Dons, 1922 (Trueba, 1980).
C. variabilis Kellicott, 1883 (p. 51).
C. variabilis var. *emarginata* Kellicott, 1883 = *C. variabilis*.
C. vas Swarczewsky, 1930 = *Vaginicola vas* (Swarczewsky, 1930) Kahl, 1935.
C. virgula Penard, 1914 = *Vaginicola virgula* (Penard, 1914) Kahl, 1935.
C. voigti (Voigt, 1902) Mereschkowsky, 1933 = *Cyclodonta bipartita* Stokes, 1885 (Matthes, 1958).

Cothurniopsis

C. annulata (Stokes, 1885) Penard, 1922 = *Cothurnia annulata*.
C. antarctica Daday, 1911 = *Cothurnia antarctica* (Daday, 1911) n. comb.
C. astaci (Stein, 1854) Entz, 1884 = *Cothurnia astaci*.
C. aurea Gajewskaja, 1933 = *Vaginicola vas* (Swarczewsky, 1930) Kahl, 1935.
C. canthocampti Monard, 1919 = *Cothurnia canthocampti* Stokes, 1886.
C. dionysii Penard, 1914 = *Pseudothuricola dionysii* (Penard, 1914) Kahl, 1935.
C. elastica Penard, 1914 = *C. valvata* Stokes, 1893.
C. entzii Stiller, 1931 = *Pyxicola entzii* (Stiller, 1931) Kahl, 1935.
C. longipes Voigt, 1902 = *Cyclodonta bipartita* Stokes, 1885 (Penard, 1922).
C. minutissima Penard, 1914 = *Cothurnia minutissima* (Penard, 1914) Kahl, 1935.
C. ovata (Dujardin, 1841) Zelinka, 1928 = *Cothurnia ovata*.
C. richtersi Penard, 1914 = *Cothurnia richtersi* (Penard, 1914) Kahl, 1935.
C. subglobosa Daday, 1911 = *Cothurnia subglobosa* (Daday, 1911) n. comb.
C. urceus Gajewskaja, 1933 = *Vaginicola vas* (Swarczewsky, 1930) Kahl, 1935.
C. valvata Stokes, 1893 (p. 52).
C. vejdovskii (Vejdovski, 1882) Zelinka, 1928 = *Cothurnia oblonga*.

Cyclodonta

Cyclodonta bipartita (Stokes, 1885) Matthes, 1958 (p. 52).

Daurotheca

D. marginata (Kellicott, 1883) Jankowski, 1987 = *Cothurnia variabilis*.
D. tespa Jankowski, 1987 (p. 54).
D. transoceanica Jankowski, 1987 (p. 54).
D. ussurina Jankowski, 1987 (p. 54).
D. variabilis (Kellicott, 1883) Jankowski, 1987 = *Cothurnia variabilis*.

Dimorphocothurnia

D. nebaliae (Dons, 1928) Jankowski, 1985 (p. 54).

Semicothurnia

S. acuta (Levander, 1915) Jankowski, 1976 = *Cothurnia acuta*.
S. amphicteis (Lang, 1948) Jankowski, 1985 = *Cothurnia amphicteis*.
S. nereicola (Precht, 1935) Jankowski, 1976 = *Cothurnia nereicola*.

Sincothurnia

S. apseudophila (Lang, 1948) Jankowski, 1985 = *Cothurnia apseudophila*.
S. auriculata (Stiller, 1939) Jankowski, 1985 = *Cothurnia auriculata*.
S. compressa (Claparede and Lachmann, 1858) Jankowski, 1985 = *Cothurnia compressa*.

S. compressula (Wailes, 1928) Jankowski, 1985 = *Cothurnia compressa.*

S. cyathiformis (Stiller, 1939) Jankowski, 1985 = *Cothurnia cyathiforme.*

S. elongata (Felinska, 1965) Jankowski, 1985 = *Cothurnia elongata.*

S. flexa (Felinska, 1965) Jankowski, 1985 = *Cothurnia auriculata.*

S. gammari (Precht, 1935) Jankowski, 1985 = *Cothurnia gammari.*

S. imberbis (Ehrenberg, 1831) Jankowski, 1985 = *Cothurnia imberbis.*

S. isonica Jankowski. Although figured by Jankowski (1985), no description of this species could be located. *S. isonica* appears to resemble *Cothurnia tekirghiolica.*

S. monoannulata (Banina & Polyakova, 1977) Jankowski, 1985 = *Cothurnia monoannulata.*

S. paguri (André, 1910) Jankowski, 1985 = *Vaginicola paguri* (Kahl, 1935).

S. patula (Fromentel, 1874) Jankowski, 1985 = *Cothurnia patula.*

S. rhabdota (Bock, 1952) Jankowski, 1985 = *Cothurnia rhabdota.*

S. sinuosa (Wailes, 1943) Jankowski, 1985 = *Cothurnia sinuosa.*

Tesnotheca

T. limnoriae (Dons, 1928) Jankowski, 1987 = *Cothurnia limnoriae.*

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Indian Ocean echinoderms collected during the *Sindbad Voyage* (1980–81): 2. Asteroidea

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Materials and methods 61
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SYNOPSIS. Fifteen species of shallow-water Asteroidea, representing nine genera in four families, are recorded from collections made during the *Sindbad Voyage* (Oman to China) from the Lakshadweep (Laccadive) Islands, Sri Lanka and Pula Wé (Sumatra).

Paraferdina laccadivensis James 1973 is re-described and a new species (*P. sohariae*) is described. Range extensions are recorded for *P. laccadivensis, Fromia nodosa* and *Thromidia seychellesensis*.

INTRODUCTION

The coral reef asteroids of the islands of the western Indian Ocean are fairly well known e.g. Aldabra (Sloan, Clark and Taylor 1979), the Seychelles (Möbius 1880, A. M. Clark 1984, Jangoux & Aziz 1984), Maldives (Clark & Davies 1966, Jangoux & Aziz 1984), Mauritius (Möbius 1880, de Loriol 1885), and Réunion (Guille & Ribes 1981).

The echinoderms of Sri Lanka (Ceylon) were described by Döderlein (1889) and H. L. Clark (1915) and of India and adjacent areas by Koehler (1910). The asteroids of the eastern half of Indonesia are also fairly well known (de Loriol 1893, Döderlein 1896, 1917, 1920, 1924, 1935, 1936, Pfeffer 1900, Engel 1938*a* and *b*, Guille & Jangoux 1978, Jangoux 1978, Aziz 1976, 1979).

However the eastern Indian Ocean is less well known; small collections have been described from the Cocos (Keeling) Islands (A. H. Clark 1950) and Christmas Island (Bell 1887, Fisher 1934 and Gibson-Hill 1947) but the Sumatran fauna is poorly known.

The present collection of 53 specimens of 15 species from the Lakshadweep (Laccadive) Islands, Sri Lanka and Pula Wé (Sumatra) will therefore help to fill some of the gaps. The collection includes one new species (*Paraferdina sohariae*) and provides range extensions for *Paraferdina laccadivensis* (from the Laccadives to Sumatra), *Fromia nodosa* (from the Maldives to Sumatra) and *Thromidia seychellesensis* (from the Seychelles to Sumatra).

The collections were made during a voyage across the Indian Ocean from Oman to China. The expedition, *Sindbad Voyage*, was undertaken in 1980–81 using a replica of an ancient Arab sailing vessel, *Sohar*. Details of the holothurian fauna collected during the *Sindbad Voyage* have already been published (Price & Reid 1985).

MATERIALS AND METHODS

Specimens were collected by one of us (A. R. G. P.) and other expedition members at localities from Chetlat island, Lakshadweep (Laccadives), Sri Lanka and Pula Wé (Sumatra). Details of sampling localities are shown in Fig. 1. Sampling was undertaken principally on coral reefs using scuba. At each locality, details of habitat type and depth range were recorded, along with the number of individuals of each asteroid species.

Material was fixed and preserved using standard methods (Lincoln & Sheals, 1979). Specimens were ientified by L. M. M. in Perth. The specimens have been divided between the British Museum (Natural History) and the Western Australian Museum (WAM) with a paratype of the new species lodged at the National Museum of Natural History (USNM). An additional specimen of *P. sohariae* from the Phuket Marine Biological Centre (PMBC), Thailand was examined.

SYSTEMATIC ACCOUNT

Throughout this account the synonymy has been confined, where possible, to a single reference from which the original

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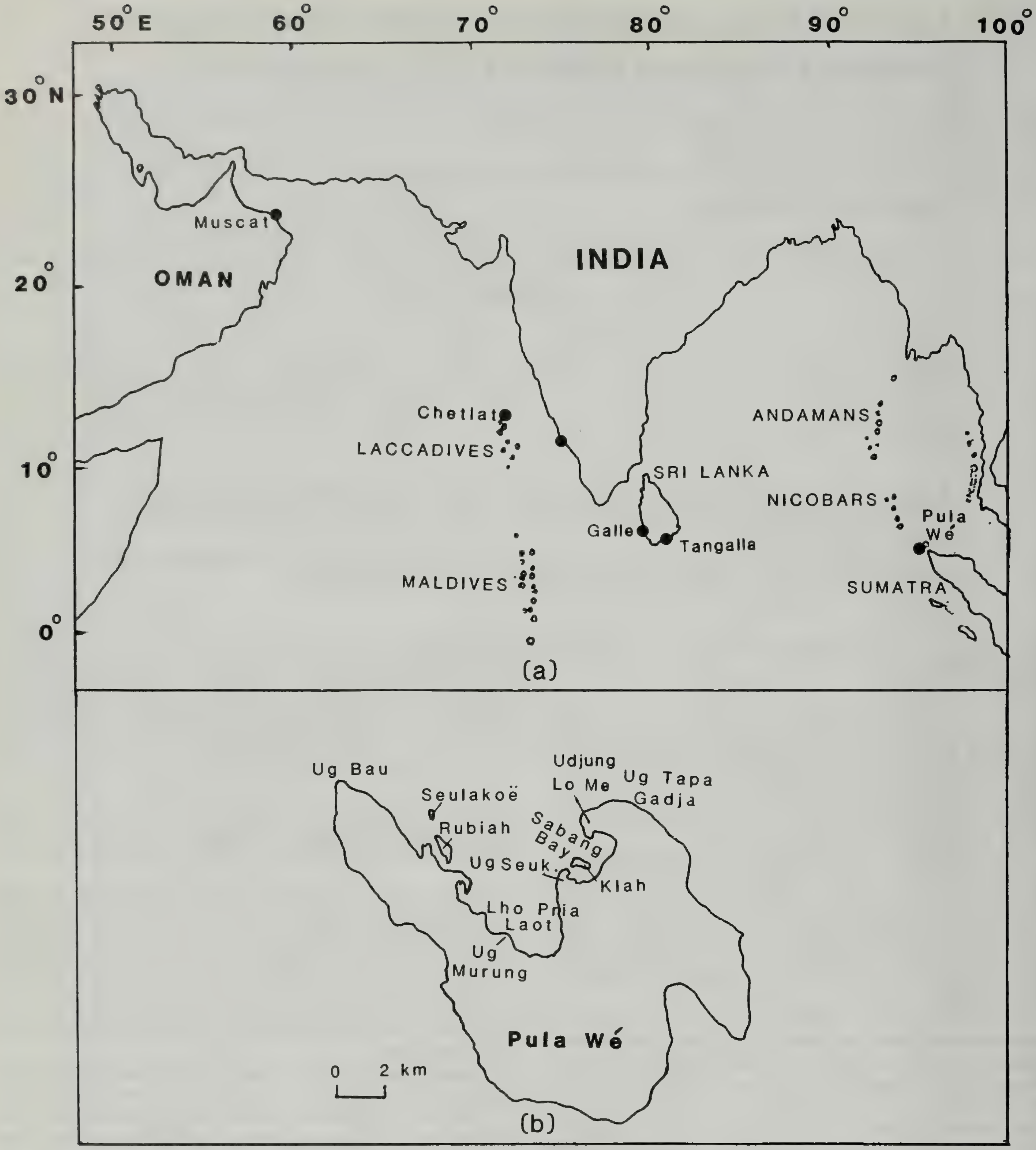
50° E
60°
70°
80°
90°
100°
30° N
20°
10°
0°
Muscat
OMAN
INDIA
Chetlat
LACCADIVES
MALDIVES
SRI LANKA
Galle
Tangalla
ANDAMANS
NICOBARS
Pula Wé
SUMATRA
(a)
Ug Bau
Seulakoë
Rubiah
Udjung Lo Me
Ug Tapa Gadja
Sabang Bay
Ug Seuk.
Klah
Lho Pria Laot
Ug Murung
Pula Wé
0 2 km
(b)

Fig. 1 (A) map of northern Indian Ocean showing sampling areas (●) during *Sindbad Voyage*, with inset (B) for Pula Wé, Sumatra.

description can be traced. Where this is not appropriate the original description is quoted.

ASTEROIDEA
OREASTERIDAE

1. *Culcita novaeguineae* Müller and Troschel, 1842.

SEE. Clark & Rowe, 1971: 34, 54, pl. 7, figs 3–5.

MATERIAL. 810425A/1 (BMNH 1989.11.1.1), 810425D/3, (BMNH 1989.11.1.3), 810424B/2, (BMNH 1989.11.1.2), 810422E/5, (BMNH 1989.11.1.5), 810504C/6, 810428E/4, (BMNH 1989.11.1.4), 810420A/9 (WAM 577–89), 810428E/3 (WAM 578–89).

COLLECTION SITES. Ug Tapa Gadja, Seulaköe, N. Klah I., E. Klah I., S. Klah I., N. Rubiah I., all Pula Wé, Sumatra (8 specimens).

HABITAT AND DEPTH. Rock, coral, sand and gravel, 2–30 m.

REMARKS. The specimens vary from those having numerous pointed tubercles on the reticulum and in the papular areas to one with no tubercles abactinally. All have coarse granules on the actinal surface and a marginal pore-free band. Specimen WAM 577–89 has a few small tubercles in the papular areas while WAM 578–89 has no abactinal tubercles at all. Both approach *C. schmideliana* in having groups of coarse granules, corresponding to the underlying actinal plates, but have small granules amongst the large ones. Their general facies is closer to that of *C. novaeguineae* than to *C. schmideliana*.

2. *Choriaster granulatus* Lütken, 1869

SEE. Clark & Rowe, 1971: 34, 53, frontispiece.

MATERIAL. 810424B/3 (BMNH 1989.11.1.6).

COLLECTION SITE. Seulaköe, Pula Wé, Sumatra (1 specimen).

HABITAT AND DEPTH. Rock, 20–35 m.

OPHIDIASTERIDAE

3. *Linckia guildingi* Gray, 1840

SEE. Clark & Rowe, 1971: 36, 61, fig. 14b, pl. 8, fig. 7.

MATERIAL. 810420A/7 (WAM 574–89) (BMNH 1989.11.1.10).

COLLECTION SITE. S. W. Klah I., Pula Wé, Sumatra (2 specimens).

HABITAT AND DEPTH. Coral reef, 4–5 m.

4. *Linckia laevigata* (Linnaeus, 1758)

SEE. Clark & Rowe, 1971: 36, 62.

MATERIAL. 810420A/6 (BMNH 1989.11.1.11), 810420A/8 (WAM 575–89).

COLLECTION SITE. S. W. Klah I., Pula Wé, Sumatra (2 specimens).

HABITAT AND DEPTH. Coral reef, 4–5 m.

5. *Linckia multifora* (Lamarck, 1816)

SEE. Clark & Rowe, 1971: 36, 62.

MATERIAL. 810124A/2a (WAM 589–89) and (BMNH 1989.11.1.12–15), 810125/B2 (BMNH 1990.4.27.13), 810423A/6 (BMNH 1990.4.27.8–9, 810423B/1 (WAM 580–89) and (BMNH 1990.4.27.5), 810423C/10 (WAM 579–89) and (BMNH 1990.4.27.6–7), 810428A/11 (BMNH 1990.4.27.10–12).

COLLECTION SITE. Ala Gala (Galle), Sri Lanka (7 specimens).

HABITAT AND DEPTH. Rock, 8–15 m.

COLLECTION SITES. Ug Bau, S. Ug Bau, Pula Wé, Sumatra (12 specimens).

HABITAT AND DEPTH. Rock, 20–40 m; coral and sand, 10–20 m.

REMARKS. Several specimens are parasitized by gastropods, *Thyca* sp. (external) and another species (? eulimid) internally.

6. *Fromia indica* (Perrier, 1869)

SEE. Clark & Rowe, 1971: 34, 62.

MATERIAL. 810124A/2G (BMNH 1989.11.1.7).

COLLECTION SITE. Ala Gala (Galle), Sri Lanka (1 specimen).

HABITAT AND DEPTH. On rock, 10–15 m.

7. *Fromia monilis* Perrier, 1875

SEE. Clark & Rowe, 1971: 36, 62.

MATERIAL. 801210B/4 (WAM 590–89) and (BMNH 1990.4.27.18).

COLLECTION SITE. S. end Chetlat, Laccadive Archipelago (2 specimens).

HABITAT AND DEPTH. Coral reef, 18 m.

REMARKS. These specimens differ from *F. nodosa* in having five plates across the base of the ray, between the superomarginals, and in lacking prominent convex carinal plates. The superomarginals are convex but do not encroach on the abactinal surface as much as in *F. nodosa*. R/r of the two specimens is 42/10 mm = 4.2/1.

8. *Fromia nodosa* A. M. Clark, 1967

SEE. A. M. Clark, 1967: 189–191, pl. 6, figs 1–3; Clark & Rowe, 1971: 36, 62, pl. 8, fig. 8.

MATERIAL. 810421A/6 (BMNH 1990.4.27.17), 810424B/1G (BMNH 1989.11.1.9), 810427D/4 (WAM 585–89) and (BMNH 1990.4.27.14–15), 810422E/2G (BMNH 1989.11.1.8), 810425F/6 (BMNH 1990.4.27.16), 810428A/11 (WAM 584–89), 810424C/1 (WAM 587–89), 810422C/2 (WAM 586–89), 810423C/10 (WAM 583–89).

COLLECTION SITES. S. Ug Bau, Ug Bau, N. Klah I., Seulaköe, N. Udjung Lo Me, Ug Seukundo, Ug Murung, all Pula Wé, Sumatra, Indonesia (11 specimens).

HABITAT AND DEPTH. Sand, coral gravel, coral and sand, rock 2–35 m.

REMARKS. The type locality of this species is Amirante Islands, W. Indian Ocean; Clark also records it from the Maldives. The range was extended to the Marshall Is. (W. Pacific) by Oguro & Sasayama (1984), but this is the first record from Indonesia. The specimens have less prominent carinal plates than the holotype but otherwise agree closely. The superomarginals are large and rounded, nearly as broad as long. There are generally only three plates across the base of the ray between the superomarginals. The specimens range in size from R/r of 42/9 mm to 31/7 mm (R/r varies from 4.1 to 5.25/1).

9. *Nardoa frianti* Koehler, 1910

SEE. Koehler, 1910: 158–161, pl. 17, figs 3, 4.

MATERIAL. 810424B/1a (WAM 573.89) and (BMNH 1989.11.1.16).

COLLECTION SITE. Seulaköe, Pula Wé, Sumatra (2 specimens, R/r = 123/12 mm (larger specimen).

HABITAT AND DEPTH. Coral gravel, 20–30 m.

REMARKS. The present specimens agree closely with Koehler's

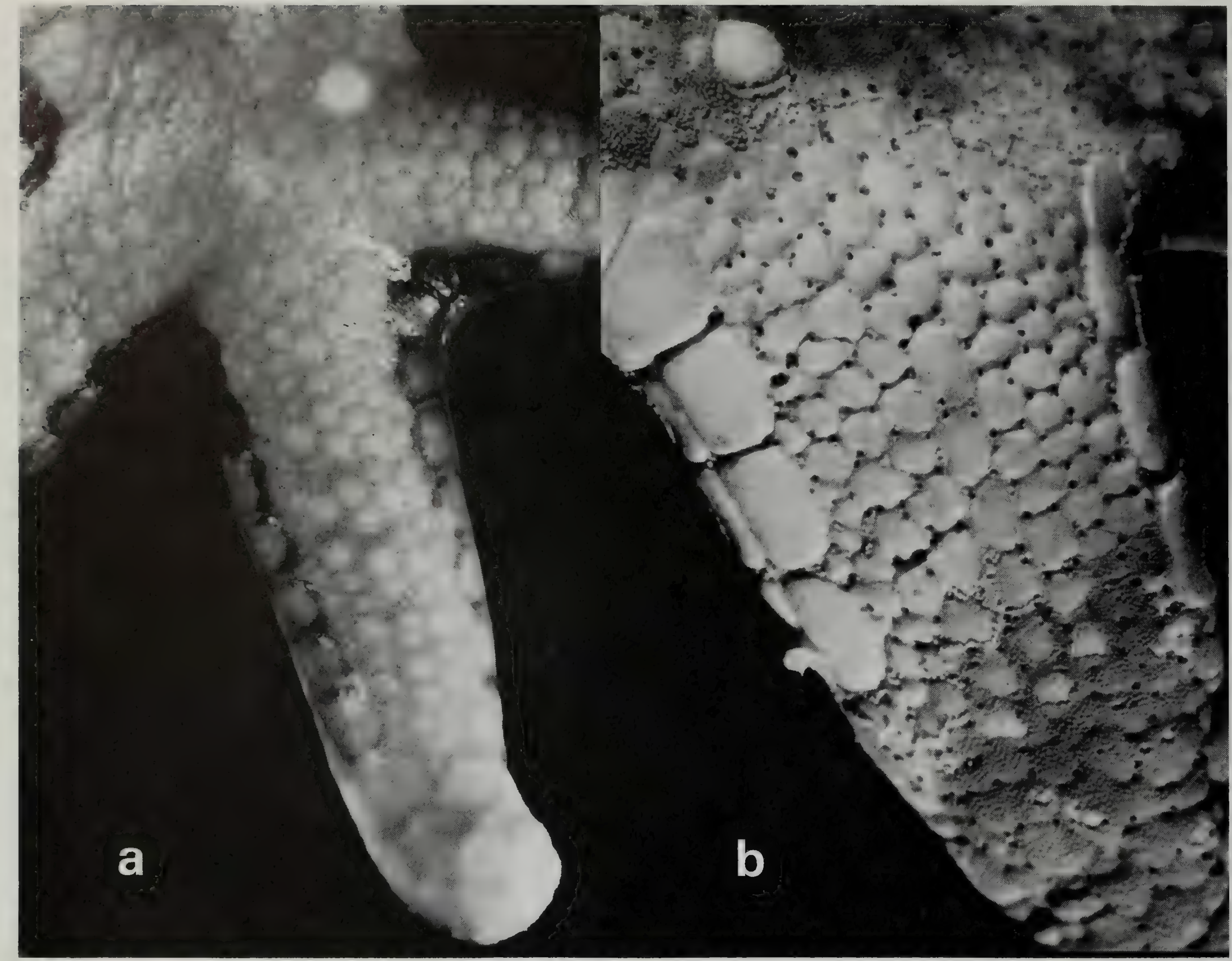

Fig. 2 *Paraferdina laccadivensis*, a, abactinal view (BMNH 1990. 4.27.1, R/r = 36/12 mm); b, abactinal surface, denuded (WAM 77–90, R/r = 33/11 mm).

description and figures. *N. frianti* differs from *N. mamillifera* Livingstone, 1930 principally in the disposition of the actinal plates. In *N. frianti* they are poorly developed and never extend to more than half the arm length. Frequently the series consists of a few plates at the base of the ray with a few more small plates between the large inferomarginals which abut the adambulacrals. If a second series is present at all it consists of a very few plates in the arm angle. In *N. mamillifera* the actinal plates are well developed with two or more rows at the base of the ray. The main series extends to about two thirds of the arm length with plates nearly as large as those of the inferomarginals in some specimens. Both species have alternating large and small superomarginal plates. *N. frianti* and *N. mamillifera* cannot therefore be considered synonymous, as suggested as a possibility by Clark and Rowe (1971).

10. *Nardoa galatheae* (Lütken, 1864)

SEE. Clark & Rowe, 1971: 36, 64.

MATERIAL. 810213A/1 (WAM 572–89), 810428B/4 (BMNH 1989.11.1.17).

COLLECTION SITES. Tangalla, Sri Lanka (1 specimen, R/r = 69/12 mm); S. Ug Bau, Pula Wé, Sumatra (1 specimen, R/r = 140/17 mm).

HABITAT AND DEPTH. On rock, 3–20 m.

REMARKS. The smaller specimen (apart from having six rays) is indistinguishable from individuals from north-western Australia, which have convex abactinal granules, while the large one has much less convex granules, similar to others of comparable size from the Moluccas. Since one of the latter has a regenerating arm with more convex granules, as found in the smaller specimen, it appears that the more convex shape of the granules is a juvenile character.

11. *Neoferdina cumingi* (Gray, 1840)

SEE. Clark & Rowe, 1971: 36, 65; Jangoux, 1973; 786–789.

MATERIAL. 810430A/39 (BMNH 1990.4.1.2), 810504B/3 (WAM 581–89) and (BMNH 1990.4.27.3), 810423C/10 (WAM 582–89), 810422E/2 (BMNH 1990.4.27.4).

COLLECTION SITES. N. Klah, N. Rubiah I., Ug Seukundo, Ug Bau, all Pula Wé, Sumatra, Indonesia (5 specimens).

HABITAT AND DEPTH. Rock, coral and sand, 2–10 m.

PARAFERDINA James 1973

Type species. *Paraferdina laccadivensis* James 1973.

Type locality. Minicoy Island, Lakshadweep (Laccadive) Islands, Indian Ocean.

For the sake of completeness James' (1973) diagnosis of this poorly known genus is repeated here.

Diagnosis. A genus of Ophidiasteridae with polygonal aboral plates, irregular in size with spaces for papular pores; superomarginal plates regular and uniformly covered by granules; actinal plates embedded in tissue; no actinal papulae; a single row of short furrow spines with tips projecting to the outside.

Remarks. *Paraferdina* differs from *Ferdina* principally in having a regular series of superomarginals and from *Neoferdina* in lacking bare plates.

12. *Paraferdina laccadivensis* James, 1973

See. James, 1973: 556–557, pl, 1a.

Material. 810428A/12 (BMNH 1990.4.27.1), 810423C/10 (WAM 77–90), 810422E/2C (WAM 76–90).

Collection sites. Ug Bau, S. Ug Bau, N. Klah I., all Pula Wé, Sumatra, Indonesia (3 specimens).

Habitat and depth. Mixed coral and sand, 2–8 m; rock 20–30 m.

Diagnosis. A species of *Paraferdina* with short, stout arms, largest known R/r is 42/13 mm, range of R/r ratio 3.0 to 3.2/1; abactinal plates irregular in shape but all of similar size, flat to slightly convex aligned along arms or irregularly arranged, 7–9 across base of ray; carinal series distinct but not prominent; superomarginal plates large, conspicuous from above, squarish to semiciruclar; actinal plates in 4–5 rows at base of ray; granules on abactinal plates uniform, 9–10/linear mm, on marginals 12/mm and on actinal plates 10–12/mm; abactinal surface uniform light orange, superomarginals magenta, arm tips cream (from one preserved specimen).

Description. (Figs 2, 3) The three specmens have R/r of 42/13, 36/12 and 33/11 mm giving R/r of 3.2 and 3.0/1. The abactinal plates are circular to irregular in shape, 1–2 mm in diameter and are notched for papulae (Figs 2a, b, 3a). They are nearly flat and vary from being aligned along the arm to being irregularly disposed particularly on the outer third of the arms; the carinal row of 18–20 plates is distinct nearly to the arm end; a few plates are slightly more convex than the remainder and in some cases are larger than the lateral plates. At the base of the ray there are 3–4 more or less distinct longitudinal rows of plates on either side of the carinal series decreasing to two distally and becoming more irregular in arrangement. On one specimen slightly raised plates form up to five indistinct rows across the arms. The terminal plate is rounded, 1.5 to 1.8 mm in diameter.

The superomarginal plates are large, conspicuous when viewed from above (Figs 2b, 3a) and number 10–11 (the third from the arm angle measures 3.0 to 3.5 mm long by 2 to 3 mm broad) and are regularly arranged except sometimes near the arm end, they vary from more or less square to rectangular and D shaped; the last superomarginals meet across the upper surface of the arm. The inferomarginals number 12–16, the smaller number when they match the superomarginals, the larger when the plates become smaller and less regular near the arm end. The actinal plates are in four rows at the base of the rays except in the largest specimen where there are 2–3 plates of a fifth row.

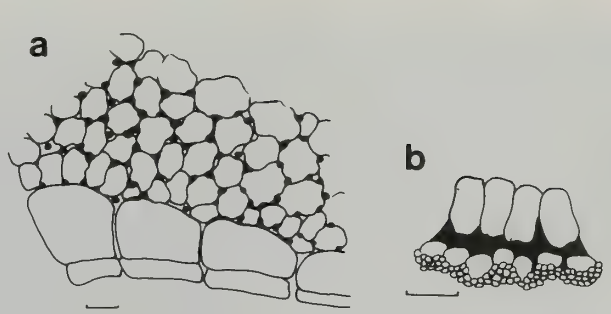

Fig. 3 *P. laccadivensis*, a, base of arm, denuded, carinal series at top, first superomarginal on left (WAM 77–90); b, ambulacral furrow, showing outer, granule covered face and inner surface of furrow spines (WAM 77–90). (Scale bar = 1 mm.)

The abactinal plates are covered by close packed, convex, polygonal granules (9–10/linear mm) except near the arm ends where they are coarser and irregular in size (5–7/mm). In the largest specimen the granules surrounding the papular pores are slightly elongate. The marginal plates have a finer granulation (12 granules/mm) while the actinal plates have 10–12 granules/mm. The adambulacral armature is limited to a single row of paired furrow spines, which are stout, blunt ended, equal to subequal in size (in one specimen measuring 0.8 by 0.5 mm) but somewhat irregular in size and shape. The actinal granulation conceals all but the tips of the furrow spines (Fig. 3b).

The papulae are generally single with 6 equally spaced around a hexagonal carinal plate; however, where the plates are less regular, papulae occur in groups of two or three and there may be up to 14 around one plate.

The colour of one specimen (preserved in Steedman's solution) is striking, the abactinal surface is light orange bordered by bright magenta superomarginals except for the arm tips which are cream. The inferomarginals and actinal areas are paler, shading to cream at the furrow; the arm ends and madreporite are cream. One dry specimen has the abactinal surface burnt orange, including the arm tips, with the marginals and actinal surface faded magenta, the largest specimen (dry) has the abactinal surface faded to deep cream; magenta is still evident on the marginals and actinal surface but the colour does not extend to the arm ends.

Remarks. The present specimens, in excellent condition, allow further descriptive details and variation of the species to be noted. The R/r ratio differs from that of the holotype which had R.r of 35/14 mm (2.5/1) (James 1973). The illustration of the holotype, however, indicates longer arms relative to r despite damage to the arm ends. Since it would have been difficult to estimate R accurately the difference in R/r ratio from the present specimens is not regarded as significant.

The major difference is in the number of superomarginal plates (15 in the holotype but no more than 12 in the present specimens) and in their shape (the holotype has the superomarginals broader than long while the Sindbad specimens have them as long as broad or longer).

In other respects these specimens closely resemble the holotype. Unfortunately direct comparison with the holotype could not be made and the Sindbad specimens are referred to this species with a little hestitation.

The colour is described for the first time.

We agree with James (1973) that this species belongs in a genus between *Ferdina* and *Neoferdina* and consider it to be more closely related to the latter because of the plate arrangement and prominent (but not bare) superomarginal plates.

13. ***Paraferdina sohariae*** sp. nov.

Ferdina offreti: (pt.) Koehler, 1910: 143, 147, pl. 16, Figs 4, 5.

HOLOTYPE. 810125A/1 (WAM 78–90).

TYPE LOCALITY. Deumba Gala, Galle, Sri Lanka, on rock 12–15 m.

MATERIAL. 810125A/1 four paratypes (WAM 79–90, BMNH 1990.4.4.2–3, USNM E40225) same data as holotype; PMBC 3048, Similan I., Andaman Sea, coral reef, 14 m, 12 Feb. 1979.

HABITAT AND DEPTH. Rock, 12–15 m; 62 m (Koehler, 1910).

DIAGNOSIS. A species of *Paraferdina* with somewhat flattened, tapering arms, largest known R/r is 50/15 mm, range of R/r ratio 3.3 to 4.3/1; abactinal plates markedly variable in shape, size and convexity, 5–7 across base of ray; usually a prominent carinal series of elevated, slightly convex plates sometimes alternating with smaller convex or flat plates; usually smaller flat plates among the larger ones on disc or arms; superomarginal plates large, conspicuous from above, D-shaped; actinal plates in 4–5 rows at base of rays; granules on abactinal plates very variable, from 5–6 to 9–10/linear mm on convex plates, 12/mm on interstitial and flat plates, 9–12/mm on actinal plates; granulation is coarser near arm ends than proximally; 1–5 enlarged granules sometimes present on convex abactinal plates; colour in life unknown, preserved specimens have buff or yellow-brown granules on the convex plates contrasting with orange to deep rose-red granules on the interstitial and flat plates.

DESCRIPTION OF HOLOTYPE. (Figs 4, 6) Rays 5, tapering, R/r = 40/11 mm, = (3.6/1), br = 11.5 mm. The abactinal surface of the disc and rays is convex, with convex, rounded to polygonal, granule covered abactinal plates and large superomarginals (Fig. 4a, b). There are 22–23 carinal plates; on the outer two thirds of the ray prominent convex carinals alternate irregularly with smaller flat plates. At the base of the ray there are five to seven plates across the arm, two or three each side of the carinal series, by about half the arm length this is reduced to one each side of the carinal series. The abactinal plates are irregular in shape and size, 0.8–2.7 mm diameter, close fitting and slightly notched for the papulae. On the disc there are five prominent primary interradial plates (including the madreporite) and a prominent radial plate at the beginning of each carinal series. The remainder of the disc is covered by smaller, irregularly arranged plates.

The madreporite is small, rounded triangular, convex, situated interradially, half way between the anus and the margin.

The superomarginals number 12–13, the first pair are wider than long (3 × 2 mm) but the remainder are about as wide as long except distally where they are again wider than long. They are prominent, more or less semicircular and gradually decrease in size distally, the last 2–4 meet mid radially. The inferomarginals number 15 and are aligned with the superomarginals except at the arm tips; they are longer than wide (3 × 1.5 mm) except for the first one which is square.

The actinal plates are in 4 rows proximally, (Fig. 4c), with a few plates of a 5th row in some arm angles. The innermost row extends nearly to the arm end (to the 11th or 12th inferomarginal), the second row extends to the 9th or 10th inferomarginal, the third row to the 6th or 7th infero- marginal and the fourth to the 3rd or 4th inferomarginal.

There is a single row of adambulacral spines along the furrow margin, only the tips of which project above the adjacent granules. The furrow spines are subequal, truncate, 1.05 mm long, two or occasionally three per plate (Fig. 6a). The four oral spines are undifferentiated from the furrow series.

The entire surface is granule covered; the abactinal convex plates are more coarsely granulated (9–10/linear mm) than the smaller plates and the marginals (12/mm). In addition some of the convex plates bear 1–5 enlarged tubercle-like granules (Fig. 6b). Near the arm ends the granulation of abactinal, terminal and marginal plates is very coarse (6–7/mm). The actinal plates have 10–12 granules/mm.

The papulae occur singly, occasionally in groups of 2, not in regular rows but around the plates e.g. there are 6–8 around a carinal plate. There are no actinal or intermarginal papulae. Pedicellariae are absent.

Colour (in alcohol).The granules covering the raised abactinal plates, marginals and actinal plates are buff, those covering the flat plates and grooves between the marginal and actinal plates are orange.

OTHER MATERIAL. The four paratypes show considerable variablility in the R/r ratio and in the number and disposition of convex abactinal plates giving a very different appearance. The colour pattern is constant but the shade of orange is darker in some.

Paratype WAM 79–90 (Fig. 5a) has R/r of 36/11 mm (3.3/1). The carinal plates do not form a regular series on all the arms, fewer of them alternate with smaller plates than in the holotype and there are more large convex plates (Fig. 6c); the arm plates are from 1–3 mm in diameter with coarse granulation on the larger plates (7–8/linear mm), finer on the smaller abactinal plates and on the actinals (10–11/mm); there are 5 plates across the base of the ray; 10–11 superomarginals and 13–15 inferomarginals. The actinal plates are in 4 rows with a few extra plates in the arm angle; the third row extends to the 5th or 6th inferomarginal, the fourth to the third inferomarginal.

Paratype BMNH 1990.4.4.2 (Fig. 4d) has R/r of 37/10 (3.7/1). The carinal series is irregular except near the end of the arms and the abactinal surface is covered by large convex plates. On the proximal half of the arm there are three irregular rows with a small plate either side on some rays. There are 13 superomarginals and 15–16 inferomarginals. The actinal plates are in 3 rows proximally, with a few plates of a 4th row.

Paratype BMNH 1990.4.4.3 is an irregular specimen with three arms regenerating. R/r = 38/10 mm (3.8/1). The abactinal plates are very irregularly arranged and the carinal series in only evident on one ray.

Paratype USNM E40225 (Fig. 5b) has R/r of 43/10 (4.3/1). The carinal series is only regular on one ray where large and small plates alternate distally. There are 5 plates across the base of the ray; 12–13 superomarginals and 16 inferomarginals. The actinal plates are in 4 rows proximally. The granulation is much coarser than on the holotype with 5–6 granules/mm on

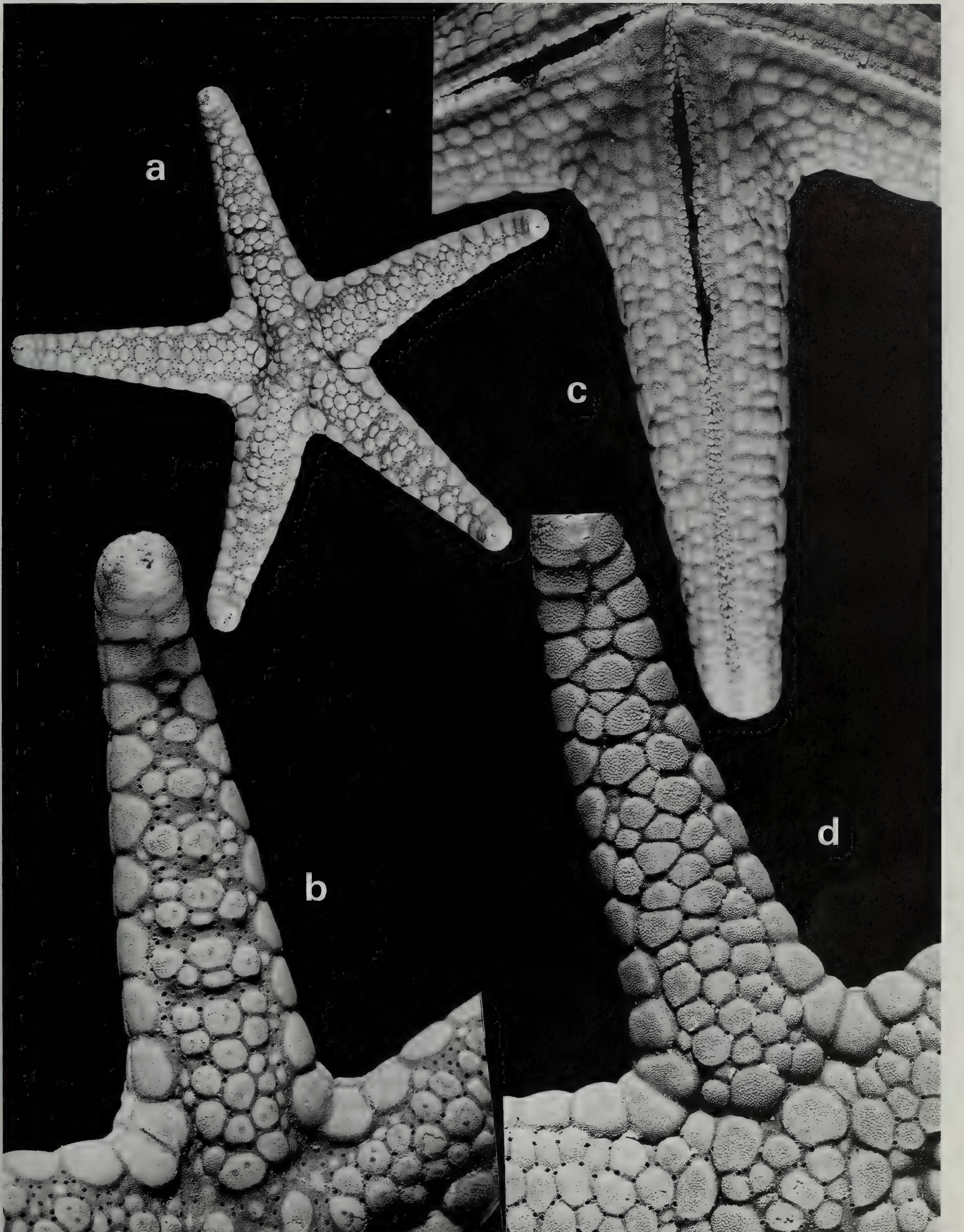

Fig. 4 *Paraferdina sohariae* n. sp. a, b, abactinal views of holotype (WAM 78–90, R/r = 40/11 mm); c, actinal view of holotype; d, abactinal view of paratype (BMNH 1990.4.4.2, R/r = 37/10 mm).

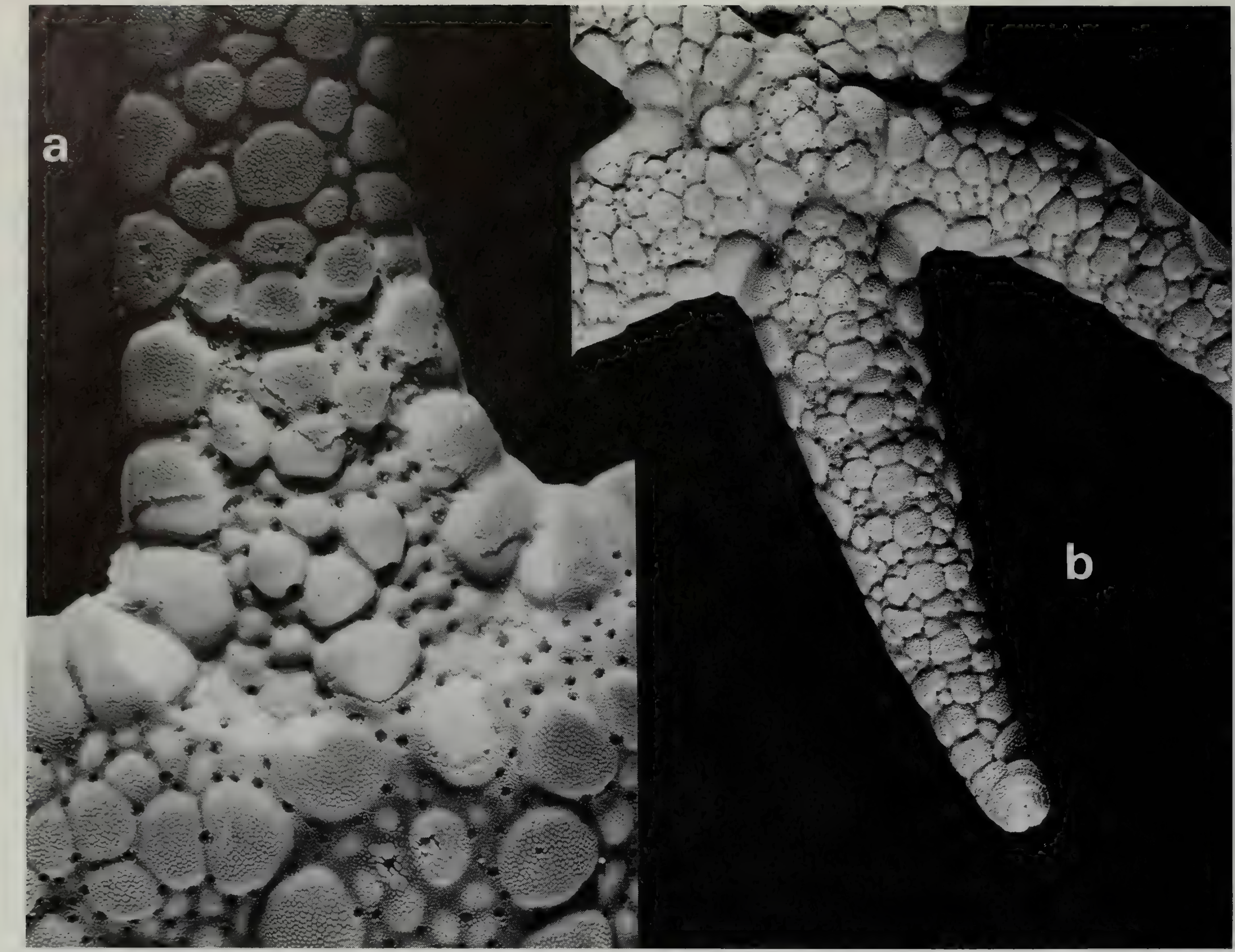

Fig. 5 *P. sohariae* n. sp. a, abactinal view of paratype, arm partly denuded (WAM 79–90, R/r = 36/11 mm); b, abactinal view of paratype (USNM E40225, R/r = 43/10 mm).

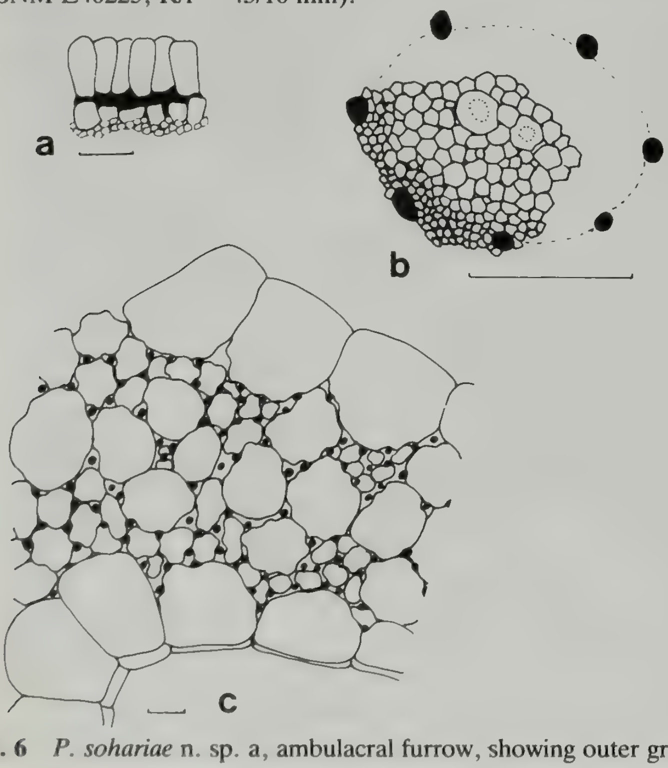

Fig. 6 *P. sohariae* n. sp. a, ambulacral furrow, showing outer granule covered face and inner surface of furrow spines (holotype, WAM 78–90); b, granulation of an abactinal plate with two tubercular granules (holotype) c, base of arm denuded (paratype WAM 79–90). (Scale bar=1 mm).

the abactinal and marginal plates with a few tuberculate granules and 9–10/mm on the actinal plates.

Only two of the paratypes have any tubercle-like granules on the abactinal plates and these are fewer than in the holotype.

PMBC 3048 (Fig. 7) has R/r of *c*. 50/15 mm (3.3/1). The R value is approximate because of damage to the arm ends. The carinal plates are enlarged, convex, alternating irregularly with smaller, flat plates. There are five plates across the base of the ray, distally three; 14 superomarginals and about the same number of infero-marginals, distally the last 2–3 supero-marginals meet across the ray.

The actinal plates are in three rows with a fourth in the arm angle, the third row extends to the fifth or sixth inferomarginal, the fourth row to the second or third inferomarginal.

The whole of the abactinal and actinal surfaces are covered by a uniform coat of fine granules, 11/linear mm.

A colour slide of the dried specimen, photographed in 1982, shows the convex abactinal plates and marginals as light yellow brown; the disc, some small plates and grooves between the convex plates and marginals were deep rose-red while the actinal plates were cream to pink outlined in old rose, yellowish at the arm ends; the furrow spines were

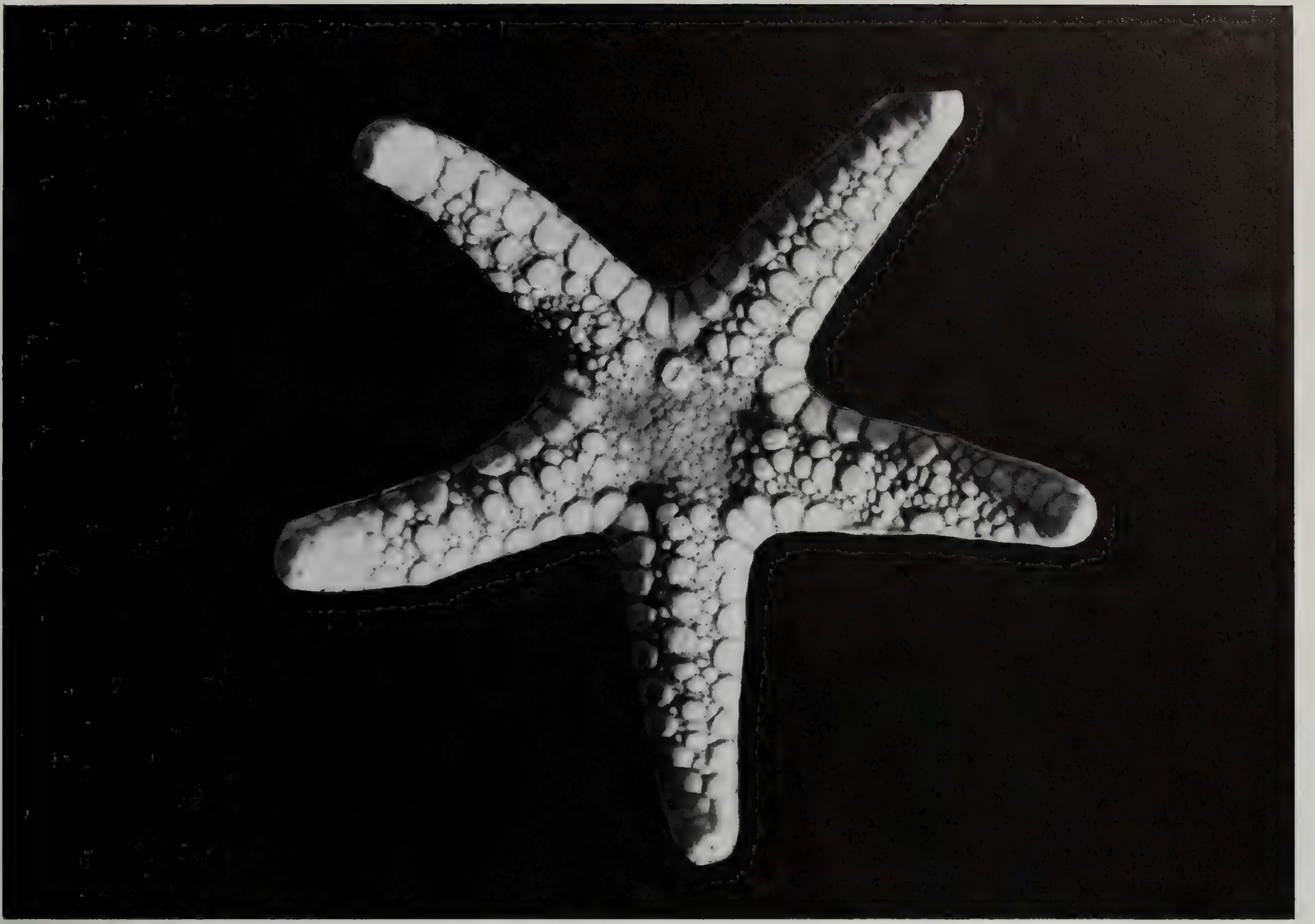

Fig. 7 *P. sohariae*, dried (PMBC 3048, R/r = 50/15 mm).

cream. This example differs from the Sindbad specimens in its larger size, lack of convex plates on the disc and uniform granulation of the plates. However, in view of the variability shown by the five specimens from Sri Lanka the differences are outweighed by the similarities and we consider that this specimen also represents *Paraferdina sohariae*.

A small specimen from Ceylon (Sri Lanka), with R of 13.5 mm, referred to as a juvenile *Ferdina offreti* by Koehler (1910) and believed to represent *Fromia nodosa* by A. M. Clark (1967) cannot be placed in *Fromia* because of the adambulacral armature. Koehler included it in *Ferdina* as it had a single row of spines on the adambulacral plates but noted that the marginal plates were granule covered, unlike those of the holotype. This specimen is now referred to *Paraferdina* and clearly represents *P. sohariae*.

RANGE OF VARIATION. The size (R) ranges from 36 to 50 mm with an R/r ratio of 3.3 to 4.3/1 (mean 3.7/1). They have five to seven plates across the base of the rays between the superomarginals, however there is considerable variation in the relative numbers of convex and flat plates. There are 14 superomarginals in the Thai specimen, 12–13 in three specimens, 10–11 in one and those of the remaining specimen are too irregular to count. Inferomarginals number 15–16 in three specimens. 13–15 in another. The abactinal plates are coarsely granulated with 9–10 granules/linear mm, while the marginals have 12/mm except near the arm ends where abactinal, terminal and marginal plates have very coarse granulation (6–7/mm). Actinal plates have 10–12 granules/mm in the holotype, 9–10/mm in one of the paratypes. Three of the paratypes have slightly coarser granulation than the holotype while one has a much coarser granule cover. The Thai specimen has a uniformly fine granule cover with 11/linear mm.

ETYMOLOGY. Named after the expedition ship, *Sohar*.

REMARKS. This species clearly belongs in the genus *Paraferdina* since it has conspicuous granule covered marginal plates, polygonal abactinal plates, irregular in size, no actinal papulae and a single row of furrow spines. *P. sohariae* differs from *P. laccadivensis* in having more tapering rays, more convex abactinal plates which are very variable in size and up to 3 mm in diameter. The differences are emphasised by the distinctive colour pattern of each species.

DISTRIBUTION. This species is known from only two localities—the type locality (Sri Lanka) and Similan I., Andaman Sea.

MITHRODIIDAE

14. *Thromidia seychellesensis* Pope & Rowe, 1977.

SEE. Pope & Rowe, 1977: 207–210, figs 7, 8, 11.

MATERIAL. 810504D/1 (WAM 576–89).

COLLECTION SITE. N. W. Klah I., Pula Wé, Sumatra (1 specimen).

HABITAT AND DEPTH. Coral rubble, 10 m.

REMARKS. The specimen is badly distorted but R/r = c. 170/50 mm (3.4/1) compared to the holotype and paratype which have R/r of 124/22.5 mm (5.5/1) and 135/27.5 mm (4.9/1) respectively. Papular areas are 2–4 mm in diameter with 20–100 pores on the disc and arm bases, decreasing to single pores near the arm ends. On the distal fifth of the arms, convex, granule covered plates form a cobbled pavement as described by Pope and Rowe. The granulation is as described for the holotype.

The present specimen with R 45 to 35 mm longer than the holotype and paratype confirms Pope and Rowe's (1977) suggestion that their specimens were not fully grown. This is the first record of this species outside the Seychelles Islands and extends the range of the species from the western Indian Ocean to the eastern Indian Ocean.

ACANTHASTERIDAE

15. *Acanthaster planci* (Linnaeus, 1758)

SEE. Clark & Rowe, 1971: 38, 71, pl. 11, fig. 3.

MATERIAL. 810424E/1 (WAM 588–89), 810425G/1 (BMNH 1989.11.1.18).

COLLECTION SITES. Nr Rubiah I., Pula Wé, Sumatra (1 specimen R/r = *c*. 150/70 mm); W. Rubiah I., Pula Wé, Sumatra (1 specimen, R/r, = *c*. 130/70 mm).

HABITAT AND DEPTH. Coral, 1.5–6 m.

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The identity and taxonomic status of *Tilapia arnoldi* Gilchrist and Thompson, 1917 (Teleostei, Cichlidae)

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SYNOPSIS The type and only specimen of *Tilapia arnoldi* Gilchrist and Thompson (1917) is redescribed (as far as its poor condition allows) and its taxonomic status reassessed in the light of that study. It is concluded that *T. arnoldi* should be considered a junior subjective synonym of *Tilapia sparrmanii* A. Smith, 1840, and not, as previously thought, of *Oreochromis mossambicus* (Peters), 1852.

INTRODUCTION

Tilapia arnoldi was described by Gilchrist and Thompson (1917) on the basis of a single specimen collected by G. Arnold from the Mazui River, Zimbabwe. Their description, although detailed, lacks a figure, and no specifically diagnostic features are given. However, in a synopsis of the Southern African cichlid species described in that paper the authors paired *Tilapia arnoldi* with a taxon then considered to be *T. melanopleura* Dum., 1859, but which is now identified as *T. rendalli* (Blgr.) 1896 (see Thys van den Audenaerde, 1964).

In Gilchrist and Thompson's synoptic key, *T. arnoldi* is distinguished from *T. rendalli* by its having a lower lateral-line scale count (27 *cf* 28–32) and a higher number of gill-rakers on the lower part of the anterior gill-arch (i.e. 15 *cf* 8–12).

Regan (1922), without examining the type specimen of *T. arnoldi*, and without giving any reasons for his opinion, suggested that '*T. arnoldi* may be a synonym of *Tilapia natalensis*' (*T. natalensis* [Weber] 1897 is now consider a synonym of *Oreochromis mossambicus* [Peters] 1852; see Trewavas [1983] for a detailed synonymy).

There matters stood until Barnard (1948*a*: 49 and 54, *b*: 448) formally synonymised *T. arnoldi* with *O. mossambicus* (then *Tilapia mossambica*). Again no reasons were given, but judging from Barnard's (1948 *a,b*) key to the southern African *Tilapia* species it was the supposed number of gill-rakers (i.e. 15) and the general morphology of *T. arnoldi* that prompted his action.

Barnard's synonymy has been accepted by subsequent workers (Jackson, 1961; Jubb, 1961, 1967), although Trewavas (1983) omits, without comment, any specific reference to *T. arnoldi* in her detailed synonymy of *O. mossambicus*. However, since she gives references, again without comment, to the Jubb and Jackson papers in that synonymy, one can assume, at least by implication, she too accepted Barnard's conclusions. Only Bell-Cross and Minshull (1988) have departed from this consensus; they list *T. arnoldi* under *T. sparrmanii* in their check-list, but give no reasons for so doing.

I have recently examined the holotype of *T. arnoldi* and, despite its now very poor condition (see Fig. 1), have concluded that it is conspecific with *Tilapia sparrmanii* A. Smith, 1840 and thus should be considered a junior subjective synonym of that species.

Throughout this paper most further references to Gilchrist and Thompson (1917) will, in the interests of brevity, be abbreviated to 'G & T', and references to the papers of Thys van den Audenaerde will be cited as 'Thys'.

MATERIAL AND METHODS

The system of counts and measurements employed follows that detailed by Trewavas (1983).

The length of the lower pharyngeal bone is measurd, perpendicularly, from the anterior tip of the blade to a horizontal line through the posterior margin of the bone's dentigerous surface; the overall breadth of the bone is taken as the horizontal distance between the outer tips of its articular horns.

Various diagnostic tilapiine features used by Thys (1964, 1968) and Trewavas (1983) at both the generic and specific levels have been used, as was information contained in the more general accounts of *T. sparrmanii, T. rendalli* (A.

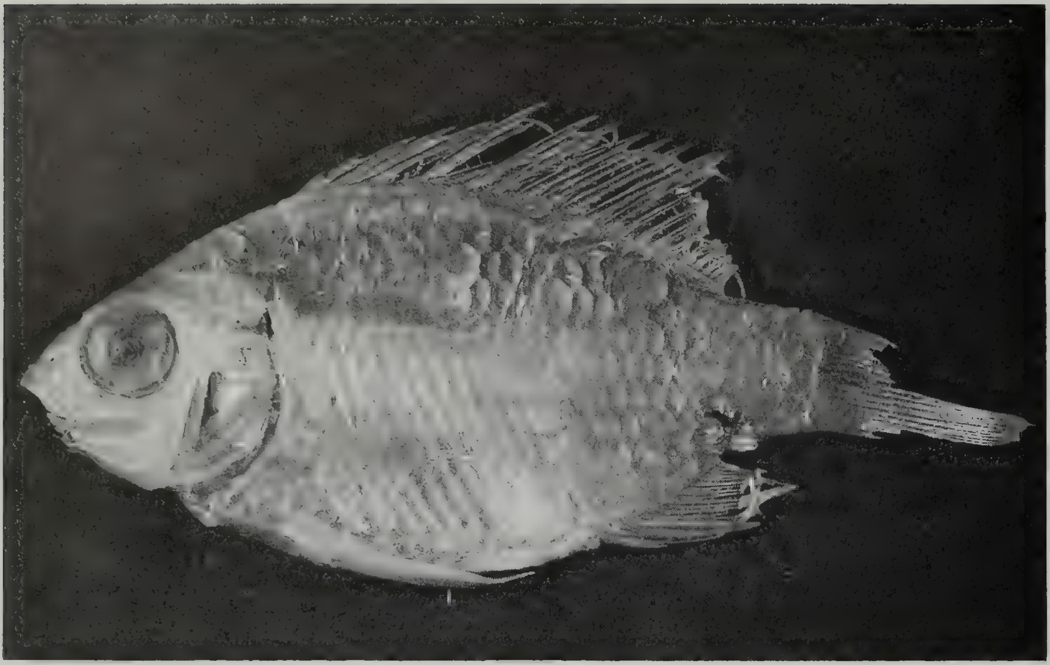

Fig. 1 *Tilapia arnoldi* holotype in left lateral view. Actual standard length: 46.0 mm.

Dum.), *T. ruweti* (Poll and Thys) and *O. mossambicus* given by Jubb (1967) and by Bell-Cross and Minshull (1988).

Specimens used for comparative purposes are:

Tilapia arnoldi: holotype, South African Museum (SAM) 10862; now housed in the Albany Museum, Grahamstown, under that number.

Tilapia rendalli: J. L. B. Smith Institute of Ichthyology, Grahamstown (RUSI) 26579; a single specimen from the Incomati river; RUSI 27988, 3 specimens from the Sabi River, Kruger National Park.

Tilapia ruweti: RUSI 30126, a single specimen from the Thamalakane River, Okovango, Botswana; 10 specimens from lot RUSI 30343, Gomoti system, Okovango, Botswana.

Tilapia sparrmanii: RUSI 22600, 3 specimens from the Palala River, Limpopo River system at Muisvogelkraal 20° 00′S, 24° 30′E, Transvaal.

Oreochromis mossambicus: RUSI 26135, 7 specimens from weir R2M 10, above Laing Dam (Fort Murray), Buffalo River system, Eastern Cape Province.

All specimens of the four latter species are of approximately the same size as the type of *T. arnoldi*, and were chosen for that reason.

REDESCRIPTION OF *T. ARNOLDI* HOLOTYPE

The specimen is now in very poor condition (Fig. 1) having at some time been partially dried-out and suffered fairly extensive damage to the body and unpaired fins. It is also partly cleared since the alimentary tract is readily visible through the body wall. No trace of chromatophores remains on the body and fins, all of which are now a light caramel-brown in colour. Unfortunately the preserved coloration and colour-patterns as described by G & T are of no taxonomic value.

The head is extensively damaged and almost detached from the body; the right operculum and suboperculum are missing, as is the entire lower jaw. Some branchiostegal rays have been lost on both sides, and the branchiostegal membrane is badly torn; the complete hyoid arch, including the urohyal is, however, present.

All four gill-arches are preserved on the left side, but only the third and fourth arches remain on the right; what seems to be the second arch of that side is detached and lies loose in the jar. The remnants of the pharyngobranchial skeleton have lost their attachment to the skull and pectoral girdle. The lower pharyngeal bone was still attached to the upper pharyngeal elements, but has now been dissected-out for detailed examination.

Damage to most of the fins is also extensive. The upper half of the caudal fin is missing and the distal portions of all but three branched dorsal fin rays broken off, as are all the branched anal rays, although these are still attached to the fin proximally. The pelvic fins are virtually undamaged, as is the right pectoral fin; the left pectoral, however, is broken distally.

With the aid of radiographs, and using the undamaged fins, the following ray counts and measurements can be made: Dorsal with 15 spinous and 11 branched rays; the penultimate and ultimate spines are the longest of the series, are of equal length, and are as long as the third anal spine. Pelvic fins 12.0 mm in length, their tips reaching the anus but not extending to the first anal spine insertion. Pectoral fin (right) *ca* 14 mm long, its tip reaching a vertical through the anus but not to that through the insertion of the first anal spine.

On the left side most scales are missing from the anterior part of the body below the upper lateral-line, but the squamation is fairly complete over the entire right side and on the posterior part of the left side. All scales are cycloid, those on the flank below the lateral-line over approximately the anterior half of the body have moderately rugose exposed surfaces. There is a very gradual transition in size between the antero-ventral scales on the flanks and those situated laterally and ventrally on the chest. Consequently the chest scales, especially in the midline, are not markedly smaller than the scales lying above them.

The upper section of the lateral-line has 15 pored scales, the lower part 11 or possibly 12; the lateral scale count is 26 or 27. There are two rows of imbricating scales on the cheeks, and these completely cover the underlying muscles. Although it is difficult to make a precise count because of damage to the caudal peduncle, there are apparently not more than 14 circumpeduncular scales. No circumpeduncular count was given by Gilchrist and Thompson, but our other counts are in close agreement except for a difference of 3 in the pored scales of the upper lateral-line.

Body measurements which could be made with any degree of accuracy are: Standard length (S. L.) 46.0 mm; head length (H. L.) *ca* 15 mm (i.e. about 33.3% of S. L.); body depth *ca* 23 mm (i.e. about 50% of S. L.). Preorbital depth 3.0 mm (i.e. about 20% of H. L.), least interorbital width 6.0 mm (i.e. about 40% of H. L.), eye, measured as the horizontal diameter of the bony orbital margin, 6.0 mm (i.e. about 40% of H. L.), depth of cheek 3.0 mm (i.e. about 20% of H. L.). Depth of caudal peduncle 1.3 times its length.

These proportional measurements, most of which were taken between bony fixed points, agree with those given by G & T, as do those for the pelvic and pectoral fins. The length (46.0 mm), however, is two millimetres less than recorded by G & T, but that difference could well be attributed to shrinkage with time, and the fact that the head is now almost free from the body.

Shrinkage and damage would not account for the difference in our counts of branched anal fin rays (11 *cf* 9 according to G & T: see p. 72 above). This discrepancy probably is due to the difficulty often encountered in deciding whether the last two or three rays of this fin are separate entities or branches of a single ray. The radiograph now available clearly shows 11 separate rays.

The gill-rakers were described by G & T as short and thick, with 15 on the lower part of the first arch. The holotype now has only the first gill-arch of the left-side remaining. The upper eight outer-row rakers on the lower (ceratobranchial) part of this arch are now fine and slender structures, the three lower rakers being short and flaccid.

Desiccation and poor preservation could well account for this alteration in gill-raker shape, but not for there being 11 instead of 15 rakers on the lower part of the arch. Since the spacing of the eleven rakers is regular and without gaps, and there is no damage to the surface of the arch, it seems very unlikely that four rakers have been lost by shrinkage or any other cause. Thus one must assume that G & T's count of 15 is an error, perhaps resulting from the inadvertent inclusion of upper (i.e. epibranchial) rakers in their count. Unfortunately that supposition cannot be checked because much of the skin covering the epibranchial has been lost and only the lowermost epibranchial raker now remains.

There also remains the problem of why Barnard (1948 *a,b*) too gave a count of 15 rakers since he had the holotype available for study. I can only proffer the suggestion that he accepted Regan's (1922) opinion, based solely on G & T's paper, and did not check the actual number of rakers.

The lower jaw of *T. arnoldi* holotype is now missing, so dental characteristics can only be determined from the premaxillary teeth. Outer row teeth on this bone are unequally bicuspid, with the very small minor cusp rather bluntly conical, and the crown of the major cusp obliquely truncate and not drawn-out. In other words, these teeth have a form common amongst many *Tilapia* and other tilapiine species (see figures in Thys, 1964, and Trewavas, 1983). Apparently no teeth are missing from this row, and their total number is 36, a figure much lower than the 'about 50 in the upper jaw' given by G & T.

Inner row premaxillary teeth are arranged irregularly in 2 or 3 series anteriorly and antero-laterally, and in a single row posteriorly. All are small and equally tricuspid.

Since the lower pharyngeal bone was still *in situ* until I removed it, one can assume that previous workers had not studied the bone in any detail, especially as none has described it or the pharyngeal dentition

The bone's dentigerous surface is broadly and almost equilaterally triangular in outline (Fig. 2). Its posterior margin is gently biconvex, with the convexities joined medially by a short and shallow concavity. The overall width of the bone is slightly greater than its length and the anterior blade slightly shorter than the median tooth row.

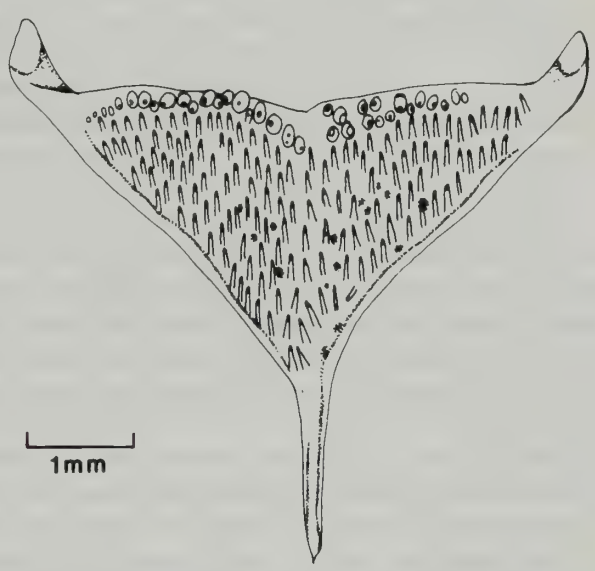

Fig 2. *Tilapia arnoldi* holotype. Lower pharyngeal bone in occlusal view. Drawn by Elaine Grant.

Except for the large, distinctly more robust and clearly bicuspid teeth of the two posterior transverse tooth-rows, all other lower pharyngeal teeth are slender and moderately spaced, are 'kukri'-shaped (see fig. 30 in Greenwood, 1987) and very weakly bicuspid.

Only one osteological character of note is revealed by the radiographs, namely that there are 27 vertebrae, comprising 14 abdominal and 13 caudal elements (including the urostylar centrum).

THE TAXONOMIC STATUS OF *TILAPIA ARNOLDI*

Because neither Regan (1922) nor Barnard (1948 *a,b)* gave reasons for, respectively, their suggested or actual synonymising of *T. arnoldi* with *Oreochromis mossambicus* it is impossible to tell what particular character or character combination shared by the two taxa led to those decisions. With hindsight it seems likely that the reasons lay mainly in the supposed number of gill-rakers in *T. arnoldi* (15 according to G & T), and possibly in its low number of cheek scale rows.

However, despite the present poor condition of *T. arnoldi* holotype, I am certain that there were only 11 rakers on the lower limb of the first gill-arch, a number below that of the fewest (14) recorded in *O. mossambicus*, and then very rarely. Furthermore, two rows of cheek scales are of rare occurrence in *O. mossambicus*, in which species three rows are modal and two rows are rarely encountered (Trewavas, 1983: 295; personal observations).

Thus neither of these features can be used to identify the specimen as *O. mossambicus*, and there are no other meristic or morphometric features of *T. arnoldi* which are diagnostic for *O. mossambicus*.

The proportions and shape of the lower pharyngeal bone in *T. arnoldi* can also be used to argue against the holotype being identified as a member of the species *O. mossambicus*. Indeed, these features indicate that the specimen is not even a member of the genus *Oreochromis* as currently defined, and that it should be referred to the genus *Tilapia (sensu* Trewavas 1983). In *Oreochromis* species the blade of the bone is as long as, and generally longer than, the median tooth row, and the bone's overall length is noticeably greater than its width (see Thys, 1964, 1968; Trewavas, 1983). In *T. arnoldi*, as in other members of the genus *Tilapia*, these ratios are reversed and the length of blade visibly contributes less to the bone's overall length than it does in species of *Oreochromis* (see Thys, 1964: fig. 5).

When the lower pharyngeal dentition of *Tilapia arnoldi* holotype is compared with that of comparable-sized *O. mossambicus* specimens, the teeth in *T. arnoldi* are seen to be more widely spaced and relatively coarser. In these respects the teeth closely resemble those of *Tilapia sparrmanii* and *T. rendalli* (whose pharyngeal bone's proportions are also like those in *T. arnoldi*).

Tilapia arnoldi also differs from *Oreochromis mossambicus* in two other features, namely its vertebral count and the size of its chest scales relative to those on the antero-ventral aspects of the flanks and anterior belly region. In *O. mossambicus* the range of vertebral numbers is from 28 to 31, with only three of the 23 specimens examined having 28 vertebrae (Trewavas, 1983). The count in *T. arnoldi* holotype is 27. The chest scales in *O. mossambicus* are noticeably smaller than those on the antero-ventral flanks and belly, whereas in *T. arnoldi* the chest scales are but slightly smaller.

Finally, mention should be made of three further features which distinguish the two species, namely the shorter pectoral fin (reaching the anus in *T. arnoldi* but to the first or second anal spine in comparable-sized *O. mossambicus*), the lower lateral scale count in *T. arnoldi* (26 or 27 *cf* 30–32), and the larger eye and wider interorbital in that species (data from personal observations and Trewavas, 1983).

Taken in concert, the characteristics discussed above strongly indicate that the type specimen of *T. arnoldi* is not conspecific with *Oreochromis mossambicus*, while, as noted earlier, the nature of its pharyngeal bone and dentition show that it is a member of the genus *Tilapia*.

If those conclusions are accepted, there remains the question of its specific identity within the genus *Tilapia*. On zoogeographical grounds and on the overall levels of morphological similarity in preserved specimens, the resolution of that problem involves comparisons with *Tilapia rendalli, T. sparrmanii* and *T. ruweti*, the two former species being widely distributed in the Zambezi system, the latter, in Zimbabwe, restricted to the Upper Zambezi river (Bell-Cross and Minshull, 1988).

Tilapia ruweti is readily distinguishable from *T. arnoldi* by its shallower body and rounded dorsal head profile, shorter and distinctly rounded pectoral fin (not reaching the level of the anus), 3 or 4 (*cf* 2) rows of cheek scales, fewer (6–8 *cf* 11) gill-rakers which also appear to be shorter and stouter in *T. ruweti* (although this difference could be a consequence of the poor conditon of *T. arnoldi* holotype) and, at least in specimens of a similar size, by its having the eye diameter about three-quarters that of the interorbital width and not equal to it as in *T. arnoldi*.

In many respects *T. arnoldi* closely resembles *T. rendalli*, but it differs in its larger scales as evidenced by the lateral scale count of 26 or 27 *cf* 29–32 in *T. rendalli*, the circumpeduncular count of 13 or 14 *cf* 16 and by the larger size of the scales on the ventral aspect of the chest. The two taxa also differ in the posterior extent of the pectoral fin which, in *T. rendalli*, reaches to the level of the first, or even the second anal fin spine, but only to the level of the anus in *T. arnoldi*. At least in specimens of a comparable size, the teeth situated anteriorly and antero-laterally in the outer premaxillary row are larger (i.e. have wider tips) than those in *T. arnoldi*, with the result that *T. rendalli* has 26–30 teeth in the outer row, whereas there are 36 in *T. arnoldi*.

None of the features distinguishing *T. arnoldi* from *T. ruweti* and *T. rendalli* serves to distinguish that species from *T. sparrmanii*, and I can find no others which do so. Furthermore the vertebral count in *T. arnoldi* (27) is that modal for *T. sparrmanii* and not for *T. rendalli* (28), although the ranges in both these species do overlap (26–28 and 27–29 for the taxa respectively).

On the basis of the similarity between *T. arnoldi* and *T. sparrmanii*, and in the absence of any detectable contradictory evidence (here the poor state of *T. arnoldi* holotype must be taken into account, as must the absence of information about its live coloration) I would conclude that *Tilapia arnoldi* Gilchrist and Thompson, 1917, should be treated as a junior subjective synonym of *Tilapia sparrmanii* A. Smith, 1840, and not, as Regan (1922) first suggested and Barnard (1948*a,b*) subsequently formalized, a synonym of *Oreochromis mossambicus* (Peters), 1852.

Acknowledgements. It is with pleasure that I thank Jim Cambray of the Albany Museum, Grahamstown for allowing me to borrow the type specimen of *Tilapia arnoldi* and other specimens described by Gilchrist and Thompson. I am especially grateful to Paul Skelton of the JLB Smith Institute of Ichthyology for the many discussions we have had about *T. arnoldi*, and for his critical reading of the manuscript. From the same Institute it is a great pleasure to thank Elaine Grant who provided the artwork, Robin Stobbs who produced the photograph and radiograph of the type specimens, and Huibre Tomlinson for her typing skills and patience when employing them.

I have benefited greatly from the generosity and hospitality of the JLB Smith Institute of Ichthyology and the Department of Ichthyology and Fisheries Science of Rhodes University, to whom I offer my warmest thanks and gratitude.

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Anatomy, phylogeny and taxonomy of the gadoid fish genus *Macruronus* Günther, 1873, with a revised hypothesis of gadoid phylogeny

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SYNOPSIS. The osteology and other anatomical features of *Macruronus* and *Merluccius* are compared; particular differences are in the structure of cranial, infraorbital, suspensorial, opercular and pelvic bones and in the vertebral column, caudal fin structure and dorsal body musculature. Presumed synapomorphies relating *Macruronus* and *Merluccius* are shown to be homoplastic. *Macruronus*, *Lyconus* and possibly *Lyconodes* form a monophyletic group recognised as family Macruronidae; *Merluccius* is the sole member of Merlucciidae. Macruronidae is considered a basal member of a monophyletic assemblage of families termed 'higher' gadoids; Merlucciidae is considered the derived sister lineage to Gadidae. The taxonomy of Macruronidae is reviewed.

INTRODUCTION

The subject of this paper is the phylogenetic position of the genus *Macruronus* which presently contains five species. Two species; *M. novaezelandiae* and *M. magellanicus* are of economic importance in the Southern Ocean and are commonly known as southern hakes, blue grenadiers or hoki in New Zealand waters and as merluza de cola around Chile and Argentina. The genus *Macruronus* is considered to belong to the family Merlucciidae along with the genera *Merluccius*, *Lyconus* and *Lyconodes*. Norman (1966) was the first author to regard *Macruronus* and *Steindachneria* as merlucciids which he assigned to a separate subfamily (Macruroninae); until then both genera had been considered as macrouroids.

Marshall (1966) identified characters suggesting unity of the Merlucciidae which also included the poorly known

Lyconus and *Lyconodes*. Marshall & Cohen (1973) removed *Steindachneria* to a monotypic family leaving four genera in the Merlucciidae. *Merluccius*, because of its economic importance, has been well-studied and Inada (1981) produced a taxonomic revision of the species, reviewed their ecology and gave detailed osteological descriptions. Inada's work has been used for anatomical comparison.

No anatomical study of *Macruronus* has been made, although Regan (1903) remarked on some osteological features. He stated that *Macruronus* was, in its cranial morphology, exactly like *Merluccius* observing that '... this correspondence extends to minute structural details, the upper surface of the skull being precisely similar in both ...' Regan's view persuaded Norman (1937) to include *Macruronus* and *Merluccius* in the same family.

Regan's observations are not borne out by the present study. There are few, other than superficial and plesiomorphic resemblances between *Macruronus* and *Merluccius*. *Lyconus* (and possibly *Lyconodes*), however, are closely related to *Macruronus* (p. 101).

These findings have led to taxonomic changes in genera comprising the Merlucciidae, to a reappraisal of the polarities of certain characters used in gadoid classification and to a revised hypothesis of gadoid phylogenetic relationships.

MATERIALS AND METHODS

The anatomical descriptions of *Macruronus* are based on specimens of three lots of *M. magellanicus*; BMNH 1936.8.26:342–351, size range, 130–250mm TL (including a cleared and alizarin/alcian stained specimen); 1936.8.26:358–363, 440–450mm TL and 1936.8.26:358–363, 700–780mm TL (including skeletal specimens); *M. novaezelandiae*; unregistered skeleton, *ca* 160mm TL. Specimens of *M. novaezelandiae* examined: 1895.4.26:1–4, 120–150mm TL and unregistered, 520mm TL. Radiographs of these specimens were used for vertebral counts.

Cleared and stained specimens, skeletons and alcohol preserved material of species representing all gadoid families have been used for comparison; details of these specimens are listed in Howes (1988). The register numbers of specimens used for the illustrations are given in the respective captions.

Abbreviations used in the figures

Unless otherwise stated, the scale bars in the figures are in mm divisions. For ease of comparison, the terms used by Inada are given in brackets.

aa	anguloarticular (angular)
aap	premaxillary articular process
ac	actinost
add	*erector + depressor analis* muscle
ahy	anterohyal (ceratohyal)
ans	'accessory' neural spine
ap	premaxillary ascending process
ar	anal fin ray
ard	anal fin radial
asp	autosphenotic (sphenotic)
av	abdominal vertebra (numbered)
bb	basibranchial (numbered)
bh	basihyal
bo	basioccipital
bof	basioccipital facet
br	branchiostegal ray
cc	cartilaginous core of exoccipital condyles
cb	ceratobranchial (numbered)
cfr	caudal fin rays
cl	cleithrum
cm	coronomeckelian bone
co	coracoid
cv	caudal vertebra (numbered)
de	dentary
dfc	diagonal frontal crest (posterior wall of sensory canal)
dh	dorsohyal (upper hypophyal)
dr	dorsal fin ray
drd	dorsal fin radial
ds	dermosphenotic
eb	epibranchial (numbered)
ect	ectopterygoid
edd	*erector + depressor dorsalis* muscle
ent	entopterygoid
epo	epioccipital (epiotic)
epu	epural
epx	*epaxialis* muscle
esa	anterior extrascapular (supratemporal)
esp	posterior extrascapular (supratemporal)
exf	exoccipital articulatory facet
exo	exoccipital
fIX	foramen for glossopharyngeal nerve
fX	foramen for vagus nerve
fc	frontal canal
fd	*flexor dorsalis* muscle
fds	*flexor dorsalis superioris* muscle
fr	frontal
fth	foramen for trigeminal and hyomandibularis nerves
fv	*flexor ventralis* muscle
fvi	*flexor ventralis inferioris* muscle
hb	hypobranchial (numbered)
hk	head kidney
hl	*hypochordal longidorsalis* muscle
hmf	hyomandibular fossa
hs	haemal spine
hsh	hypural segment of hypaxial muscle
hy	hypural (numbered)
hyo	hyomandibular
hyx	*hypaxialis* muscle
ic	intercalar
icv	intercalated vertebra
ihy	interhyal
io	interorbital (numbered)
iop	interopercular
ird	*interradialis* muscle
imp	intermuscular process of hyomandibular
lb	Baudelot's ligament
le	lateral ethmoid
lew	lateral ethmoid wing
lfc	lateral frontal crest
lia	interneural arch ligament
lip	interopercular-preopercular ligament
liv	intervertebral ligament
ls	*lateralis superficialis* muscle
mc	Meckel's cartilage
me	mesethmoid
mec	mesethmoid cartilage
met	metapterygoid

mfc	medial frontal cavity (mucuous cavity)
na	nasal
nac	neural arch
nll	lateral line nerve
nns2	second neural spine nerve
ns	neural spine (numbered)
nX	vagus nerve
op	opercular
oph	opercular process of hyomandibula
pa	parietal
pah	parhypural
pal	palatine
pb	pelvic bone
pbb	pharyngobranchial; numbered (pharyngeal)
pbp	postpelvic process
pc	postcelithrum
pcr	procurrent caudal ray
phy	posterohyal (epihyal)
pmp	postmaxillary process of the premaxilla
poh	preopercular process of hyomandibula
pop	preopercular
pp	parapophyses
pr	pleural rib
pro	prootic
ps	parasphenoid
psm	parasphenoid medial process
psp	parasphenoid ascending process
pte	pterotic
pts	pterosphenoid
ptt	posttemporal
pu	preural vertebra; numbered
qu	quadrate
ra	retroarticular
re	rostrodermosupraethmoid (mesethmoid)
rt	replacement tooth
sb	swimbladder
sc	scapular
scl	supracleithrum
so	supraoccipital
sop	subopercular
sy	symplectic
tp	tooth patch
tse	transverse septum
u	ural centrum; numbered
vh	ventrohyal (lower hypohyal)
vo	vomer (prevomer)
X	X-bone (dorsal radial)
Y	Y-bone (anal radial)

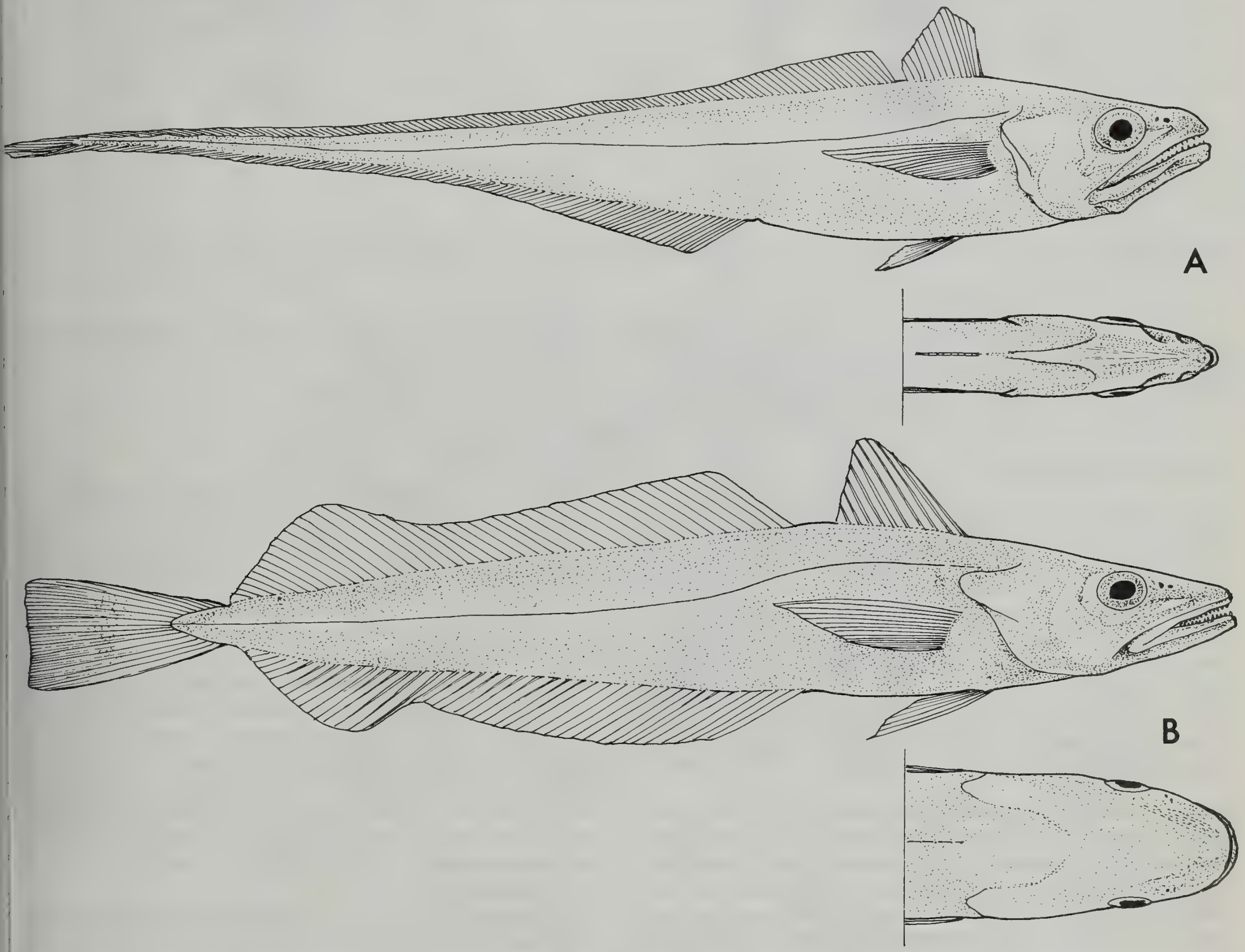

Fig. 1 A. *Macruronus magellanicus*; B. *Merluccius merluccius*, both showing the lateral aspect of the fish with dorsal views of the head region. Drawn from specimens (A) BMNH 1936.8.26: 342–351, 205mm TL, (B) 1963.5.14: 118, 280mm TL.

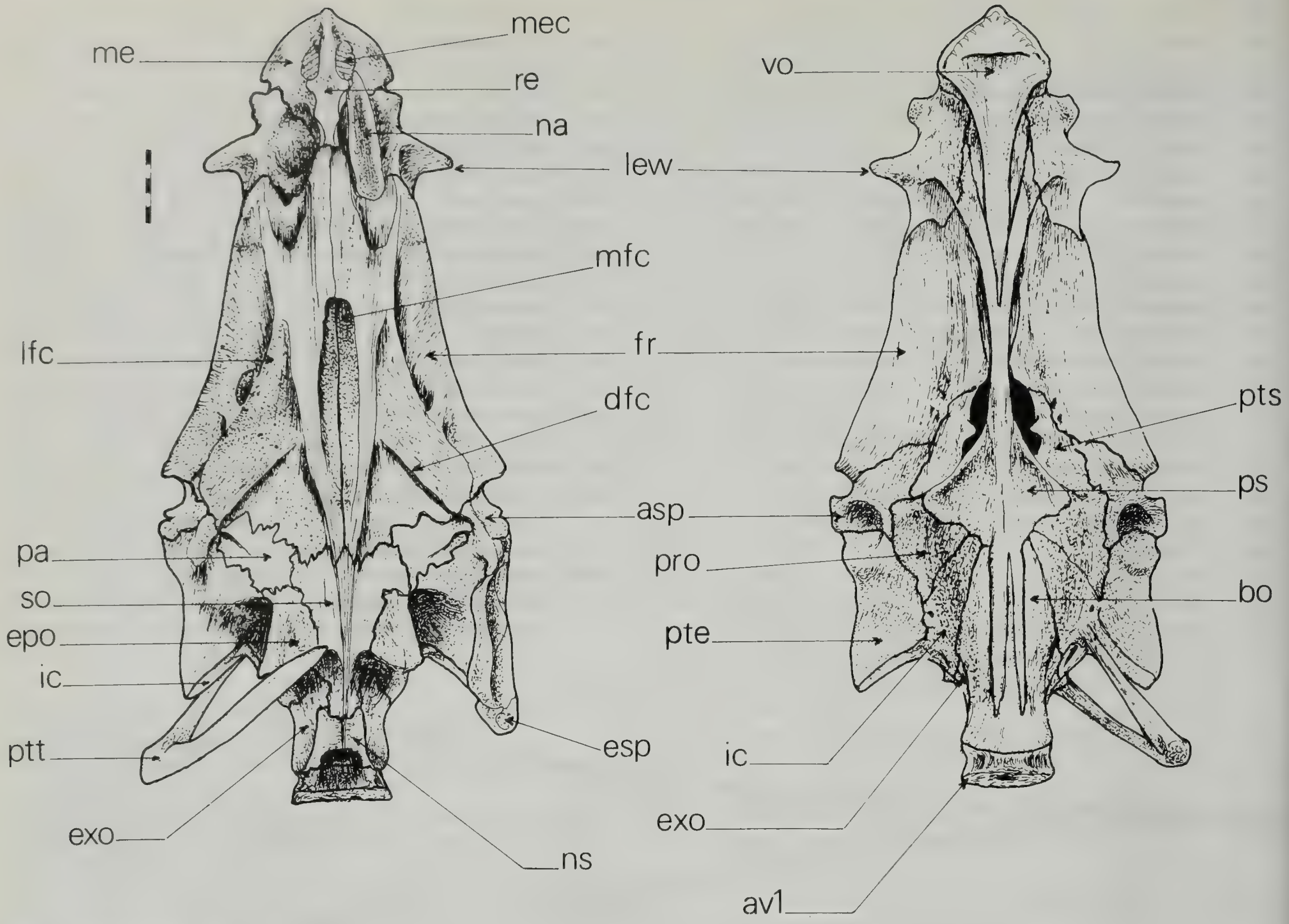

Fig. 2 *Macruronus magellanicus*, neurocranium in (left) dorsal and (right) ventral views. BMNH 1936.8.26: 352–7 (skeleton).

ANATOMY OF *MACRURONUS* AND COMPARISON WITH *MERLUCCIUS*

External morphology (Fig. 1)

Macruronus: Body elongate, strongly compressed with tapered tail. Two dorsal fins separated by slight gap; first short-based, the second confluent with caudal fin. Pectoral fins situated high, level with centre of eye; pelvic origin below or somewhat posterior to pectoral origin. Anal fin extends along posterior half of body and either confluent with, or separated by indentation from, caudal fin rays. Upper caudal rays often extended. Head relatively short (16.6–19.5% TL), jaws oblique, snout short. Opercular border not attenuated and closely attached to body wall. Scales thin and deciduous. Blue coloration.

Merluccius: Body moderately compressed with typical symmetrical gadoid tail. Two dorsal fins, the second with posterior rays extended, not confluent with caudal fin. Pectoral fins low on body, level with lower border of eye. Pelvic origin anterior to pectoral. Anal fin with posterior rays extended and not confluent with caudal fin. Head long (24.4–33.5% SL), jaws straight or slightly oblique, lower jaw projecting, snout long. Operculum with attenuated, unrestricted, posterior border. Scales thin and deciduous, ellipsoidal. Silver coloration.

Cranium (Figs 2–9)

Cranial shape:

Macruronus; characterized by cranial depth, relatively short otic and occipital regions and anteriorly tapered roof. *Merluccius*; cranium depressed, particularly where frontals meet ethmoid region; otic and occipital regions elongate, cranial roof nearly oblong. Detailed differences are:

1. *Ethmoid region*:
Macruronus (Figs 2 & 3). Dorsal ethmoid surface (rostrodermosupraethmoid) narrow and cruciform, sloping ventrally at 45° with ethmoid bloc (mesethmoid) separated from vomer by shallow cartilage. Lateral ethmoid short with concave laminate outer margin, ventrally produced into strong triangular lateral process. Vomer thick, arrow-shaped, ventral surface crossed transversely by deep recess; single row of incurved, unicuspid teeth on either side (7–8 in *M. magellanicus*; 12–15 irregularly arranged in *M. novaezealandiae*).

Merluccius (Figs 5A,C). Rostrodermosupraethmoid thick, only anterior part slopes ventrally (at an angle of 65°), cruciform part remaining horizontal. Lateral ethmoid long, outer margin thick, straight, with slight ventral lateral

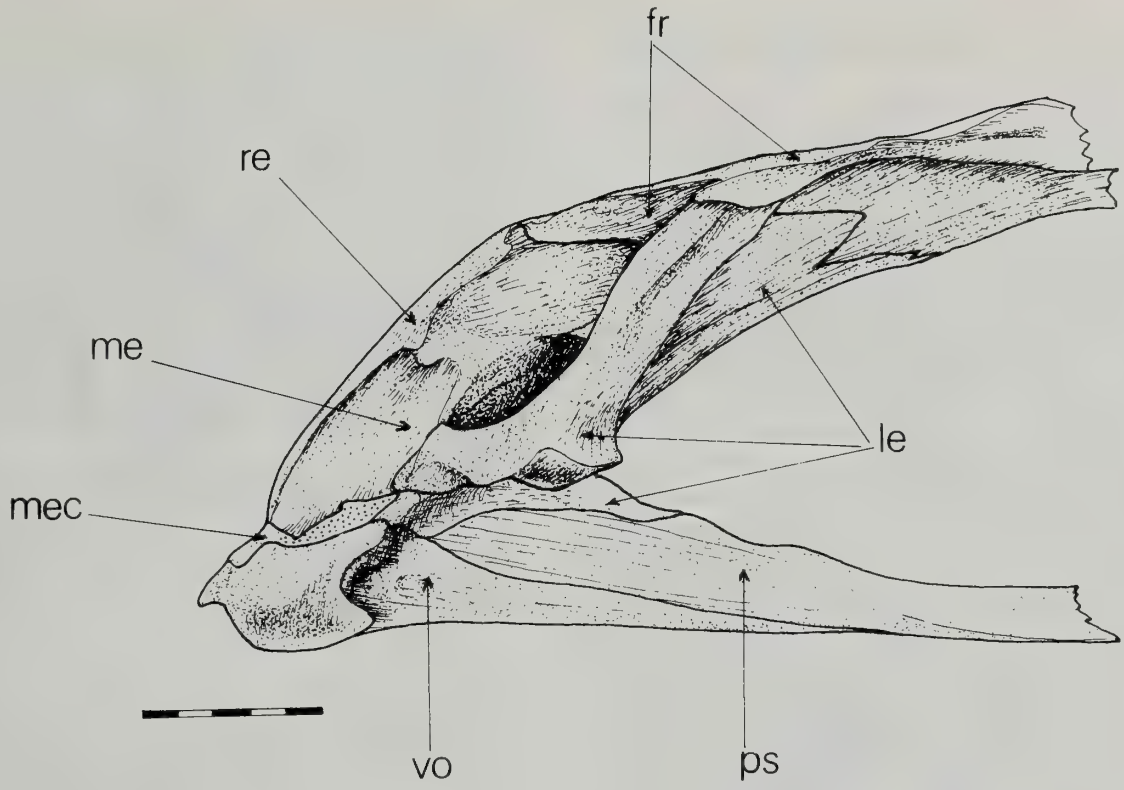
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Fig. 3 *Macruronus magellanicus*, ethmoid region in lateral view (same specimen as in Fig. 2).

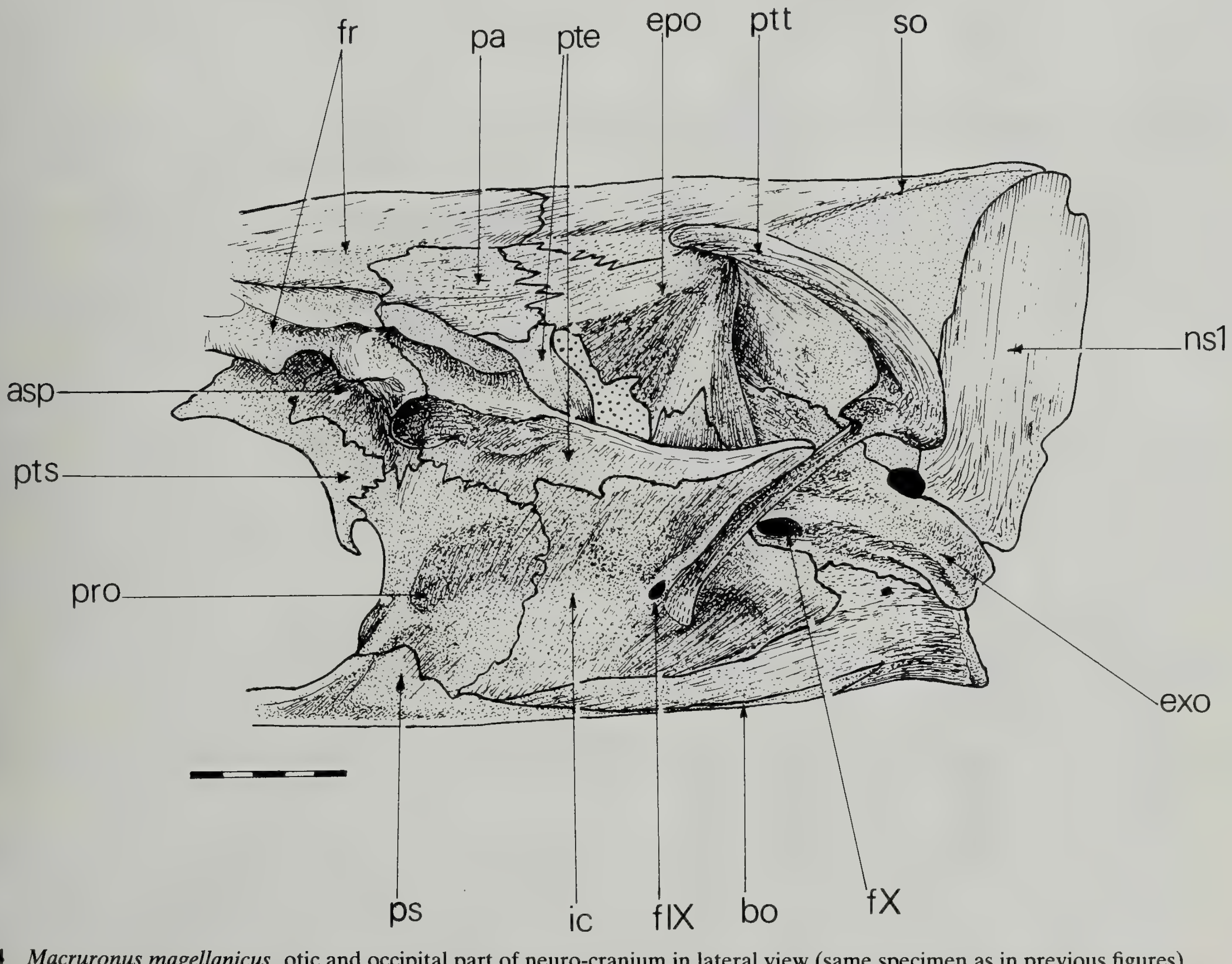
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Fig. 4 *Macruronus magellanicus*, otic and occipital part of neuro-cranium in lateral view (same specimen as in previous figures).

process. Vomer thin, bluntly triangular with dependent rim of thin bone; two rows of long incurved teeth on either side, 12–16 in outer, 6–7 in inner row.

In both genera nasals equally developed as long, shallow troughs of thin bone situated on either side of ethmoid.

2. *Orbital region*:
Macruronus (Figs 2;4). *Frontals* broadly triangular, each with irregular and indented anterior border. Posterolaterally, frontal contacts dermosphenotic which lies in a notch formed partly by the frontal margin. Bony channel of frontal sensory canal broad with an extensive anterior opening communicating with nasal. There are two lateral openings, the anterior one opens by a medial foramen into a central cavity. The broad, canopy-like roof covering frontal canal rises dorsomedially as a strong crest which continues rising posteriorly to meet its partner anterior to their junction with supraoccipital. Frontals sink between the crests forming deep V-shaped central cavity (so-called mucous cavity). Posteromedially, frontal surface forms sloped platform between high medial crest and diagonal crest which provides posterior wall of sensory canal. Ventrally, frontals bear medially curved, converging lamina which form an open groove for olfactory tracts. *Parietals* are short and broad, without crests.

Pterosphenoid small, oblong with short, somewhat medially curved, ventral processes which forms a dorsomedial support for trigeminal nerve tract (Fig. 4).

Parasphenoid circular in cross-section, narrow in orbital region but deepening anteriorly where it meets lateral ethmoids; the shallow, long ascending processes curves outward to meet prootic, intercalar and basioccipital (Fig. 4).

Merluccius has subrectangular frontals with gently convex margins above lateral ethmoids (Fig. 5). A strong crest runs diagonally from anterolateral margin to join its partner on the supraoccipital, forming a broad V. Medial wall of supraorbital (frontal) canal formed by short crest (wrongly termed the 'suborbital' by Inada, 1981), which runs parallel to the frontal margin and divergent to central frontal crest to become confluent with pterotic crest. Ventral laminae extend from the anterior part of each frontal and run parallel to one another. Parietals long and narrow in some species (Inada, 1981).

Pterosphenoid similar in size and shape to that of *Macruronus* but ventrally meets ascending process of parasphenoid and lower rim of prootic; parasphenoid square in cross section, with flat ventral surface, anteriorly it rises gently to meet lateral ethmoids.

3. *Otic region*:
Macruronus (Fig. 4). *Autosphenotic* small with strut-like lateral surface, ventrally indented with major part of hyomandibular fossa. Dorsally only small area of autosphenotic contributes the cranial surface, lying laterally between frontal and pterotic. Lateral border concave and, with the curved margin of the frontal forms a deep notch which accommodates a small, thimble-like *dermosphenotic* (see also p. 102).

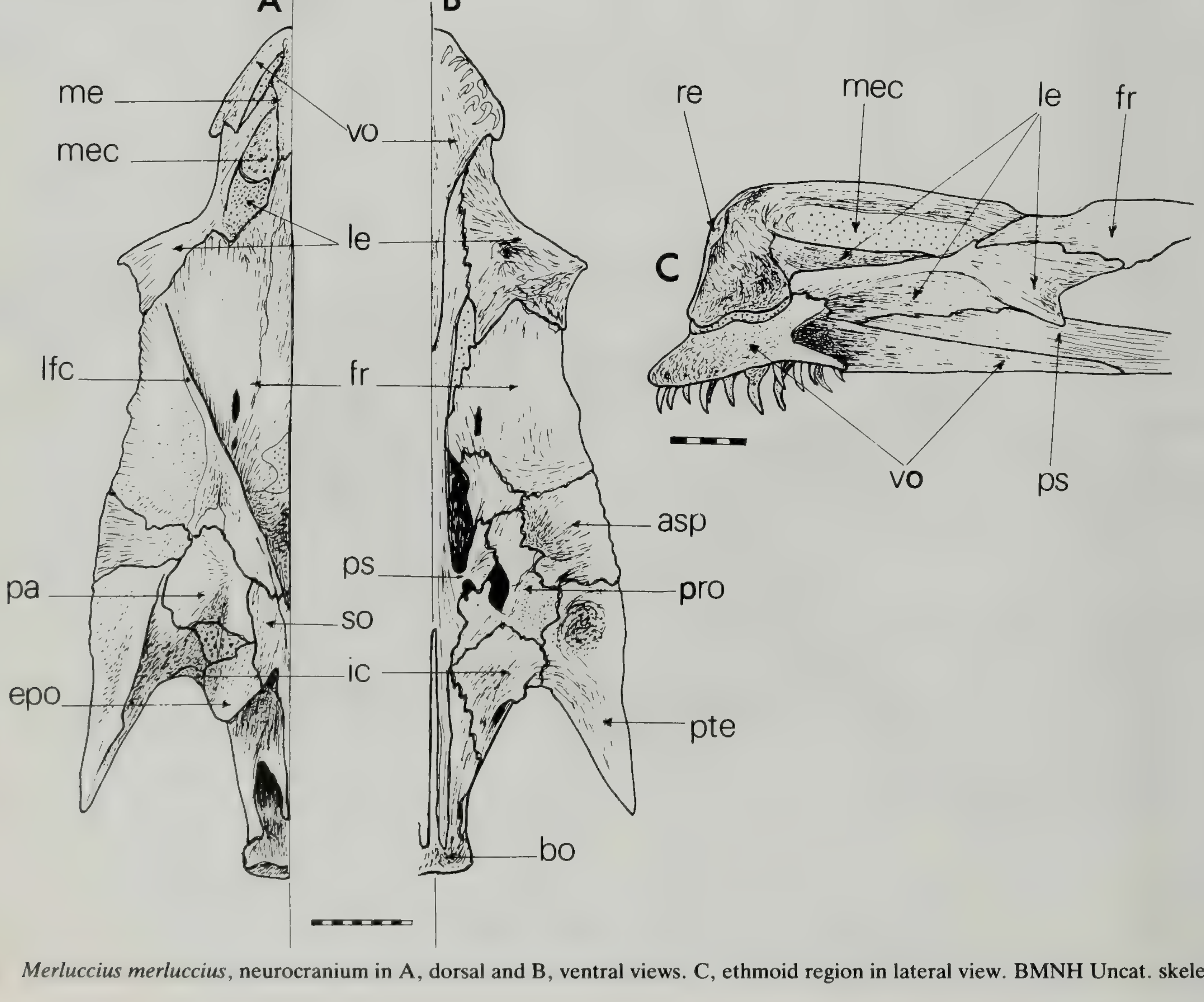

Fig. 5 *Merluccius merluccius*, neurocranium in A, dorsal and B, ventral views. C, ethmoid region in lateral view. BMNH Uncat. skeleton.

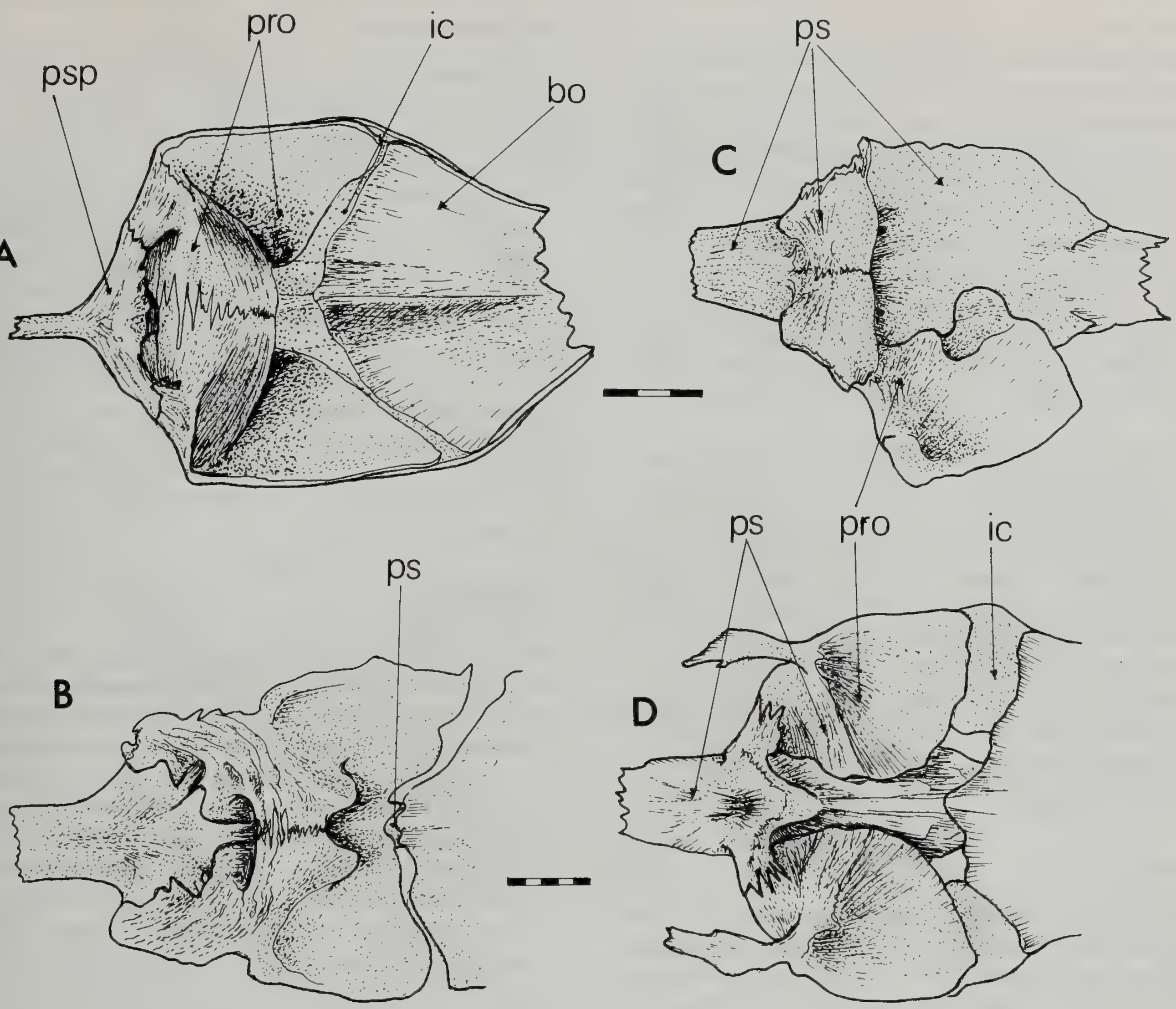

Fig. 6 Dorsal views of the cranial floor of A, *Macruronus magellanicus* (BMNH 1936.8.26: 352–7); B, *Merluccius merluccius*; C, *Mora moro*; D, *Merlangius merlangus*. (B-C from Ford collection of unregistered skeletal material).

Pterotic shallow but broad; posterolaterally meets intercalar and together they form a broad, slightly outwardly directed wing. Pterotic bears anterolaterally part of hyomandibular fossa; anterodorsally its roof bears a ridge forming the medial wall of the sensory canal which runs across its dorsoposterior region. Large area of cartilage separates medial border of pterotic from epioccipital wherein is formed the *posttemporal fossa*.

Prootic short and deep, medial margin thickened. Anteroventrally, at junction with parasphenoid ascending process, its wall is greatly thickened and extends medially to contact that of opposite side, forming a thick transverse bony septum with a convex posterior face. Anterior face of septum indented at ventral midline by shallow fossa but there is no posterior opening into the cranial cavity (Fig. 6).

Intercalar large, rising posteriorly to form laterally directed wing, posterior margin of which continues ventrally as a ridge down body of bone; anterior to base of ridge is the glossopharyngeal nerve foramen, posterior to which is the process which supports the posttemporal limb. Medially, the intercalar rises as a thin bony margin to the exoccipital (Figs 6 & 9).

Merluccius has a larger autosphenotic which presents a much greater exposed area between frontal and pterotic (Fig. 5A). Pterotic bears a larger portion of hyomandibular fossa than in *Macruronus* and, unlike that taxon, forms the entire posterolateral cranial wing. Posteromedially pterotic is deeply depressed but the cartilage separating it from the epioccipital is not as extensive and consequently the posttemporal fossa is not as deep as in *Macruronus*.

Prootic more inflated and notched or perforated by foramen for trigeminal nerve trunk (Fig. 8). The size and shape of foramen variable; in some specimens it perforates prootic wall, in others it indents margin; anterior rim of foramen provided by pterosphenoid (see Inada, 1981:71–2 for an illustrated account of variability). As in *Macruronus* each prootic is joined to its partner across the midline by a transverse bony extension. However, the extension is shelf-like with a concave posterior margin and does not contact the prootic floor thus leaving a tunnel through which run the rectus muscles (Fig. 6).

Intercalar has more extensive contact with parasphenoid, and extends further ventrally and posteriorly than in *Macruronus*. Most noticeably, it does not form the posterior boundary of the lateral cranial wing (Fig.8).

Saccular otolith: *Macruronus* (Fig. 7). Otolith thin and oblong with squared-off rostrum and irregularly rounded caudal margin. Its medial surface convex, ostium and cauda broad and shallow, containing small colliculi. Saccular otolith of *Merluccius* differs in elongate, oval outline, entire crenulate dorsal margin and narrower ostium and cauda. The hyaline-zone features of the *M. novaezelandiae* otolith have been described and used in age determination by Kuo & Tanaka (1984*d*).

4. *Occipital region*:
Macruronus (Fig. 9). *Epioccipital*, tall, semi-pyramidial with depressed cartilaginous medial face, posttemporal articulates with its dorsoposterior surface. *Exoccipital* shallow, containing in its anteroventral margin a large foramen for vagus nerve. Posteriorly, paired condyles extend and curve slightly downward on either side of foramen magnum. *Basioccipital* shallow anteriorly, flooring most of the posterior part of cranium; meets parasphenoid ventrally along a narrow V-shaped groove. *Supraoccipital* with moderately developed median crest and steeply-sloped sides meeting parietals and exoccipitals. Posteriorly, crest extends as a thin lamina gripped between the anteriorly extended halves of first neural spine.

Occipital region of *Merluccius* differs in several respects from that of *Macruronus* (Figs 6 & 8). Epioccipital is shorter and broader; exoccipital shallower and larger with an almost horizontal crest terminating in the articular condyle with vagus nerve foramen situated in lateral centre of bone. Basioccipital posteriorly longer than that of *Macruronus* but terminates anteriorly below intercalar-posttemporal process whereas that of *Macruronus* extends anteriorly. Supraoccipital longer and broader with more acutely sloped crest. According to Inada (1981:68), although there is variability in crest height among *Merluccius* species it is not sufficient to indicate specific identity.

Posttemporal

Macruronus (Fig. 9). Broad V-shaped element with thin arched horizontal limb attaching proximally to epioccipital; limb's distal surface forms facet which articulates with supracleithrum. Ventral limb also narrow, lies adnate to sloped, free border of intercalar to articulate with slight posterolateral process as base of intercalar border. *Merluccius* has narrowly V-shaped posttemporal (Fig. 8), its upper limb straight and broadly expanded where it articulates with supracleithrum; ventral limb thin and separated from posterior margins of pterotic and intercalar. Unlike *Macruronus* both upper and lower limbs of the posttemporal are aligned in nearly the same vertical plane so that the lower arm is displaced both posteriorly and medially from the pterotic-intercalar wing.

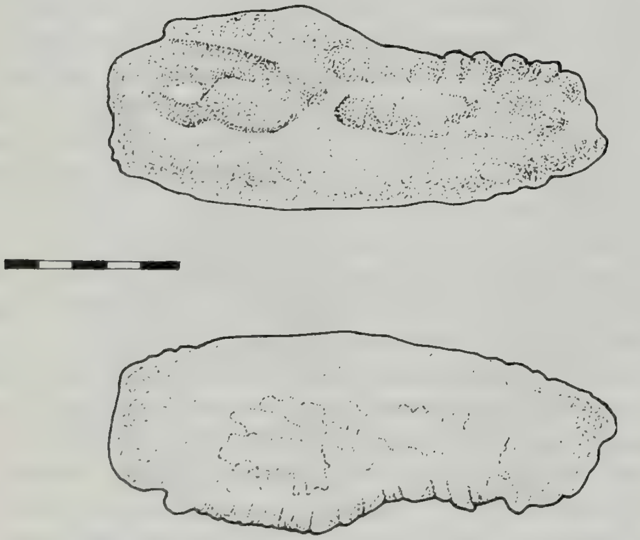

Fig. 7 Sagittal otolith (from left side of cranium) of *Macruronus magellanicus* (BMNH 1936.8.26: 358–363), showing (above) medial and (below) lateral faces; anterior is toward the left.

Extrascapulars

Extrascapulars (supratemporals) are four in *Macruronus* and *Merluccius*. In *Macruronus* all are confined to lateral margin of the cranium, above the pterotic (Figs 2 & 9); in *Merluccius* two extrascapulars lie medially along inner side of horizontal posttemporal limb. In *Macruronus* the posterior extrascapular is circular with a dorsolateral flange, that preceding is long and oblong covered only by skin; above and anterior to it lies the largest of the four, having a narrow dorsolateral flange abutting the anterior element which lies above the sphenotic and communicates directly with the frontal branch of supraorbital canal. The space between first and third extrascapulars occupied by band of thick connective tissue running from medial surface of large second element to attach to pterotic rim. In *Macruronus* it seems the large, third extrascapular has moved laterally with respect to that in *Merluccius*.

Infraorbitals

Macruronus (Fig. 10) has six infraorbitals; 1st elongate with, halfway along its length, a shallow ascending process which articulates with lateral surface of lateral ethmoid wing; 2nd infraorbital triangular, posteriorly expanded where it meets the 3rd which is almost square, occupying the corner of the series; 4th small, circular with deep outer flange covering sensory canal; 5th elongate, boomerang-shaped with sensory canal entirely enclosed. Unlike the other infraorbitals, this bone is densely ossified with a solid posterior flange.

Merluccius has five infraorbitals (Inada, 1981). Most noticeable differences are taller articular process of 1st infraorbital which articulates with ventral surface of the lateral ethmoid wing; deeper and smaller 2nd infraorbital; larger 3rd and 4th, and smaller 5th. All infraorbitals are partially covered along their orbital borders by an ossified flange leaving the remainder of the infraorbital sensory canal covered only by skin (the usual condition among gadoids). Only in *Macruronus* and *Lyconus* is the sensory canal of 5th infraorbital completely enclosed (condition in *Lyconodes* unknown).

Upper and lower jaws (Figs 11 & 12)

Macruronus has relatively short upper jaw. *Premaxilla* with tall ascending and articular processes and short, rounded postmaxillary process. Two rows of teeth, outer row 16–17, long, medially curved; inner row *ca* 35, minute, lying flat and medially directed, the last *ca* 10 being evenly spaced, others irregular. *Maxilla* has tall articular head with a broad, deep, medially directed process; posterodorsal process rises gently from halfway along the bone and has vertical posterior margin separated by short distance from distal tip of the maxilla. Maxillary tip with slight ventroposterior prolongation.

Merluccius has a long upper jaw. Premaxilla with short, sloped ascending process and long-based articular process; postmaxillary process tall, backwardly sloped. Two rows of teeth, those of inner series almost same length as those of outer and are recurved and depressible. Inada (1981) stated that there are 40–50 teeth on each side, possibly referring to total numbers of inner and outer row teeth. However, in *Merluccius merluccius* examined there are 27–30 in both outer and inner rows (total of *ca* 60). Maxilla has low articular head with a broad, shallow, medially directed process; posterodorsal process indicated only by a slight posterior elevation of

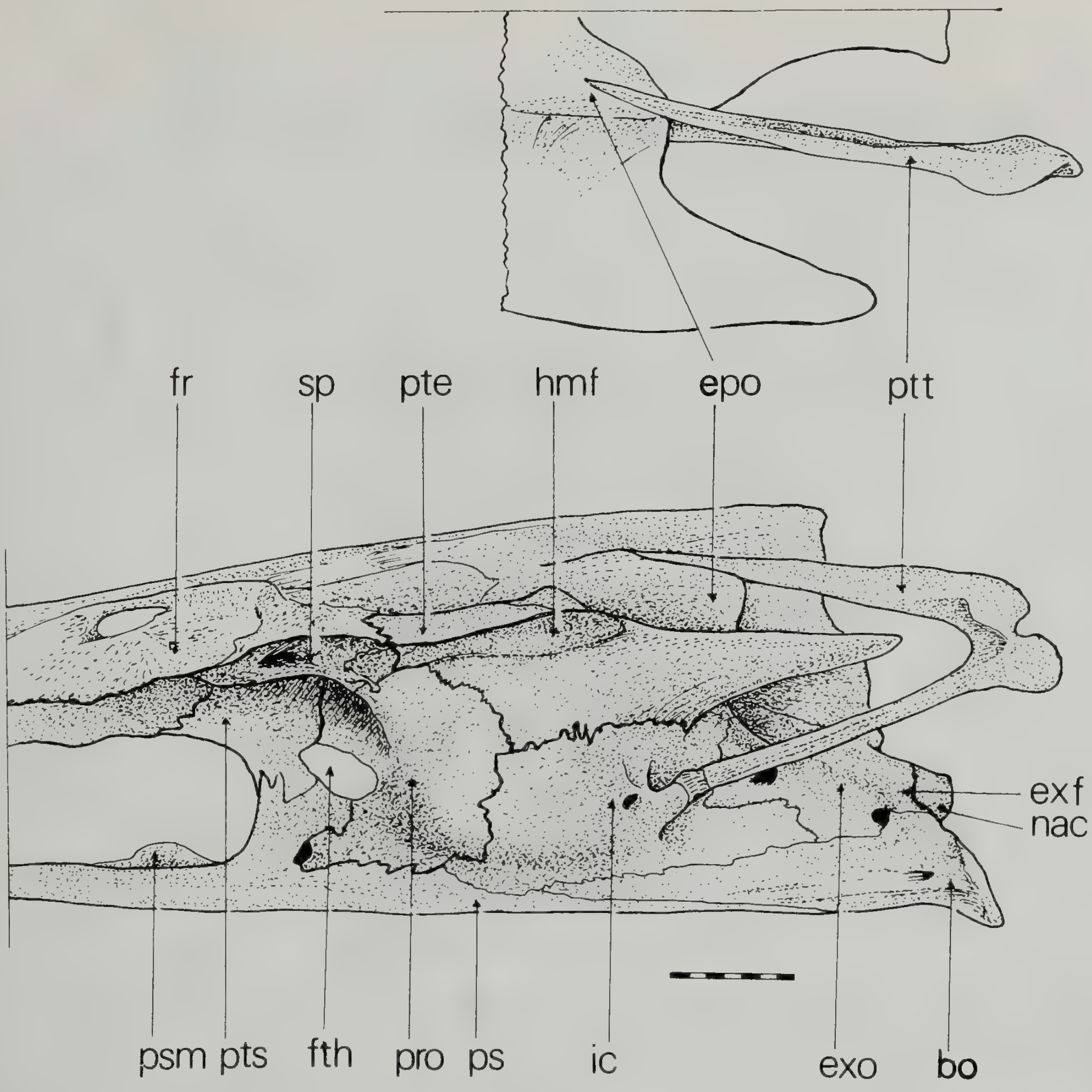

Fig. 8 *Merluccius productus*, otic and occipital part of neurocranium in lateral view; above, dorsal view of the posttemporal showing its near parallel alignment with the midline, cf. Fig. 2. (BMNH 1896.9.25: 6, skeleton, ex: Stanford University Collection).

the bone and its concave posterior margin. Distal tip of maxilla triangular to truncate, directed ventrally.

Lower jaw of *Macruronus* short and deep; *dentary* with deep anterior cavity housing mandibularis section of *adductor mandibulae* muscle; posterior border of cavity vertical. Single row of 15–20 long, widely spaced teeth. *Anguloarticular* has sloped dorsoposterior border with a tall articulatory condyle, its anterior vertical margin narrowly separated from dentary. *Retroarticular* L-shaped, its horizontal, ventral part extending forward along ventrolateral margin of dentary for almost a third of that bone's length (Fig. 12A).

Lower jaw of *Merluccius* long and shallow, dentary with long anterior mandibularis cavity, but with a sloped posterior border. Teeth in two series; Inada (1981) gives a count of 30–40 for the outer row. In *Merluccius merluccius* examined there are 30–33 outer and 30–40 inner teeth. Retroarticular is wedge-shaped element lying medial to posteroventral corner of anguloarticular (Fig. 12B). In both *Macruronus* and *Merluccius* the coronomeckelian cartilage is well-developed but the coronomeckelian bone is a minute element lying on its dorsoposterior surface. An anteroventrally extended retroarticular similar to that of *Macruronus* occurs elsewhere in gadoids only in *Lyconus*.

Labial ligament (Howes, 1988:8) well-developed, extending from anterolateral face of dentary to attach to distal surface of maxilla (Howes, 1988, fig. 17). In *Merluccius* labial ligament also well-developed but stems from mid-lateral face of dentary.

Suspensorium

Macruronus (Fig. 13). *Palatine* elongate with narrow anterior premaxillary prong; ventrally indented with deep fossa from which originates anterior part of the *adductor mandibulae* A1b muscle; medially contacts lateral process of mesethmoidal portion of the lateral ethmoid (Howes, 1987: fig. 3A). *Ectopterygoid* deep and folded laterally along its length so forming deep gutter contiguous with ventral depression of palatine; posteriorly forked, one arm extending ventrally along quadrate's medial border as far as its condyle, other, shorter arm extends posterodorsally to lie medial to metapterygoid. *Entopterygoid* large, medially sloped, contacting parasphenoid along its dorsal border; posteriorly narrowly separated from hyomandibular. *Metapterygoid* small, triangular, its apex extends dorsally to meet anterior lamina of hyomandibular. *Quadrate* fan-shaped with deep posteroventral extension which articulates medially with *symplectic*. Latter elongate with an expanded dorsal head narowly separated by a band of cartilage from the hyomandibular stem.

Hyomandibular long with a concave dorsal border, articular process rod-like and accommodated by sphenotic fossa. Opercular process relatively short, lying below dorsal level of the bone. Foramen for hyomandibular branch of facial nerve perforates anterior lamina and is exposed laterally. Entire length of posterior border of hyomandibular stem contacts preoperculum.

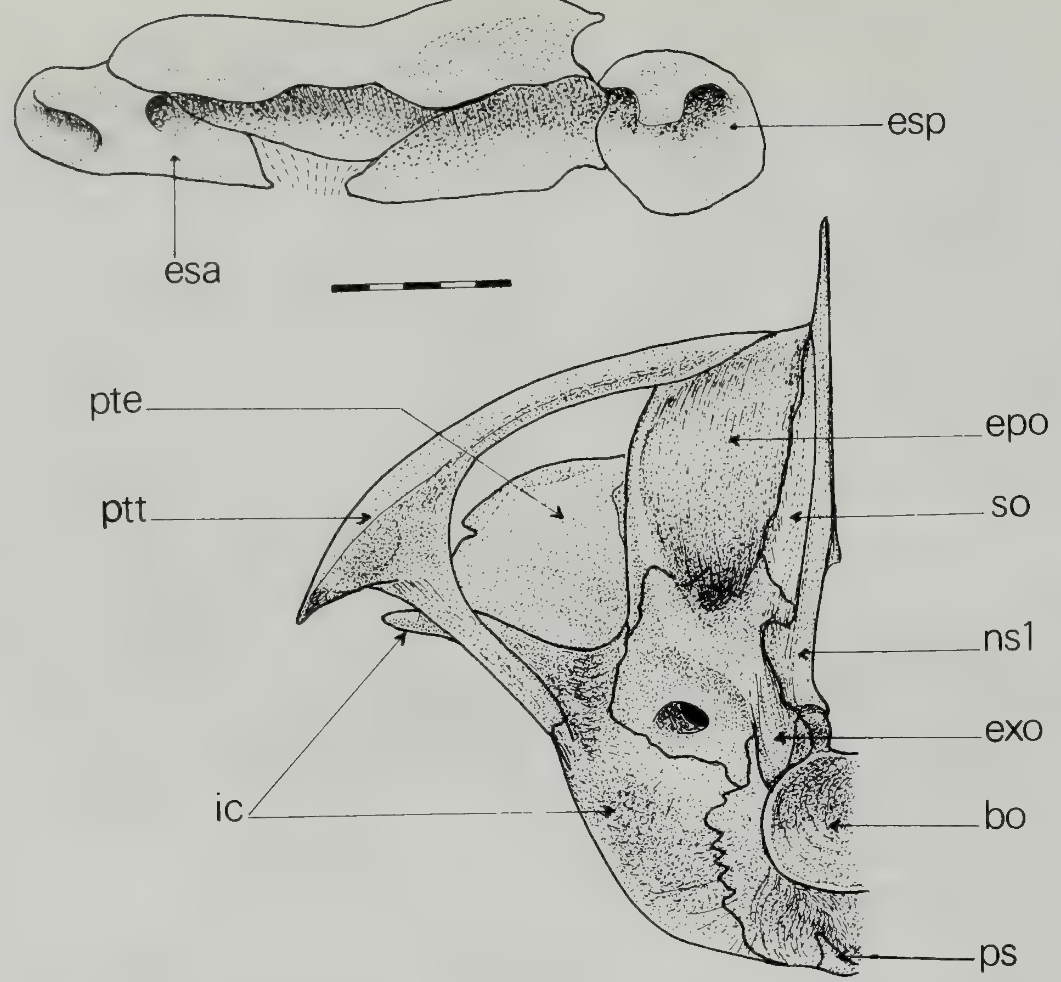
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Fig. 9 *Macruronus magellanicus*, posterior view of neurocranium and posttemporal, and (above) lateral view of the extrascapular series of the left side. (BMNH 1936.8.26: 352–7.)

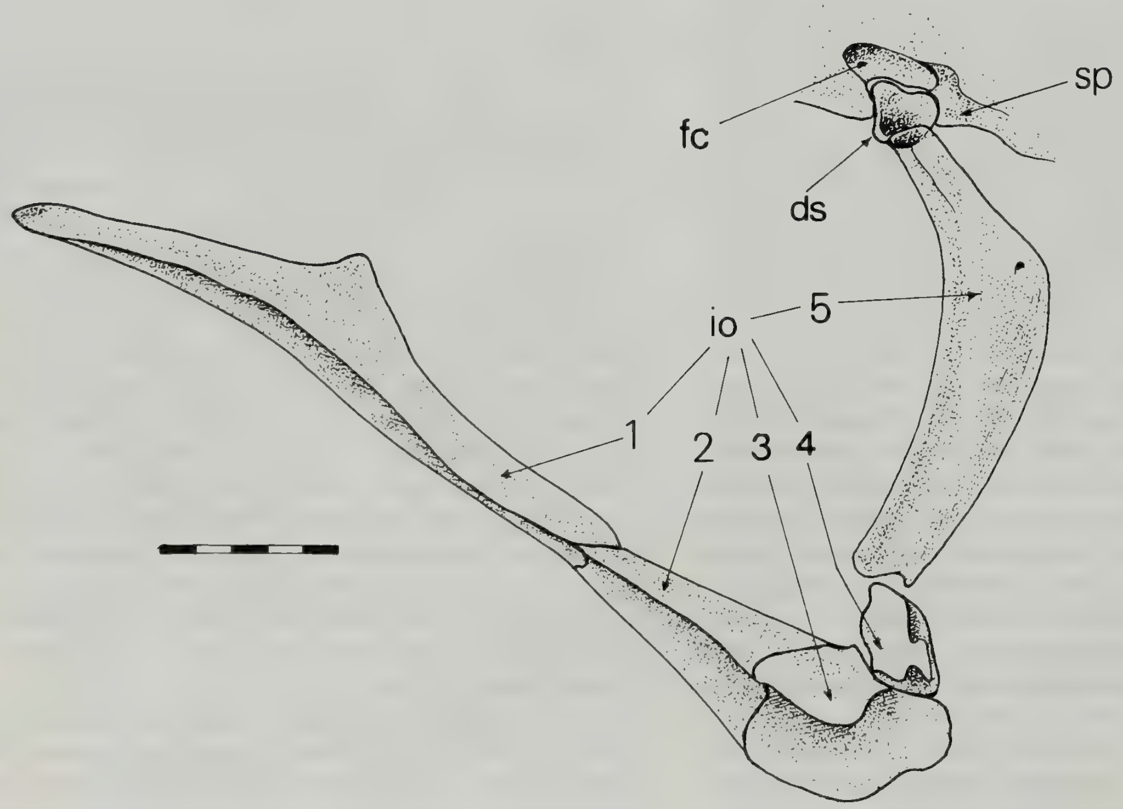
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Fig. 10 *Macruronus magellanicus*, infraorbital series (BMNH 1936. 8.26: 352–7).

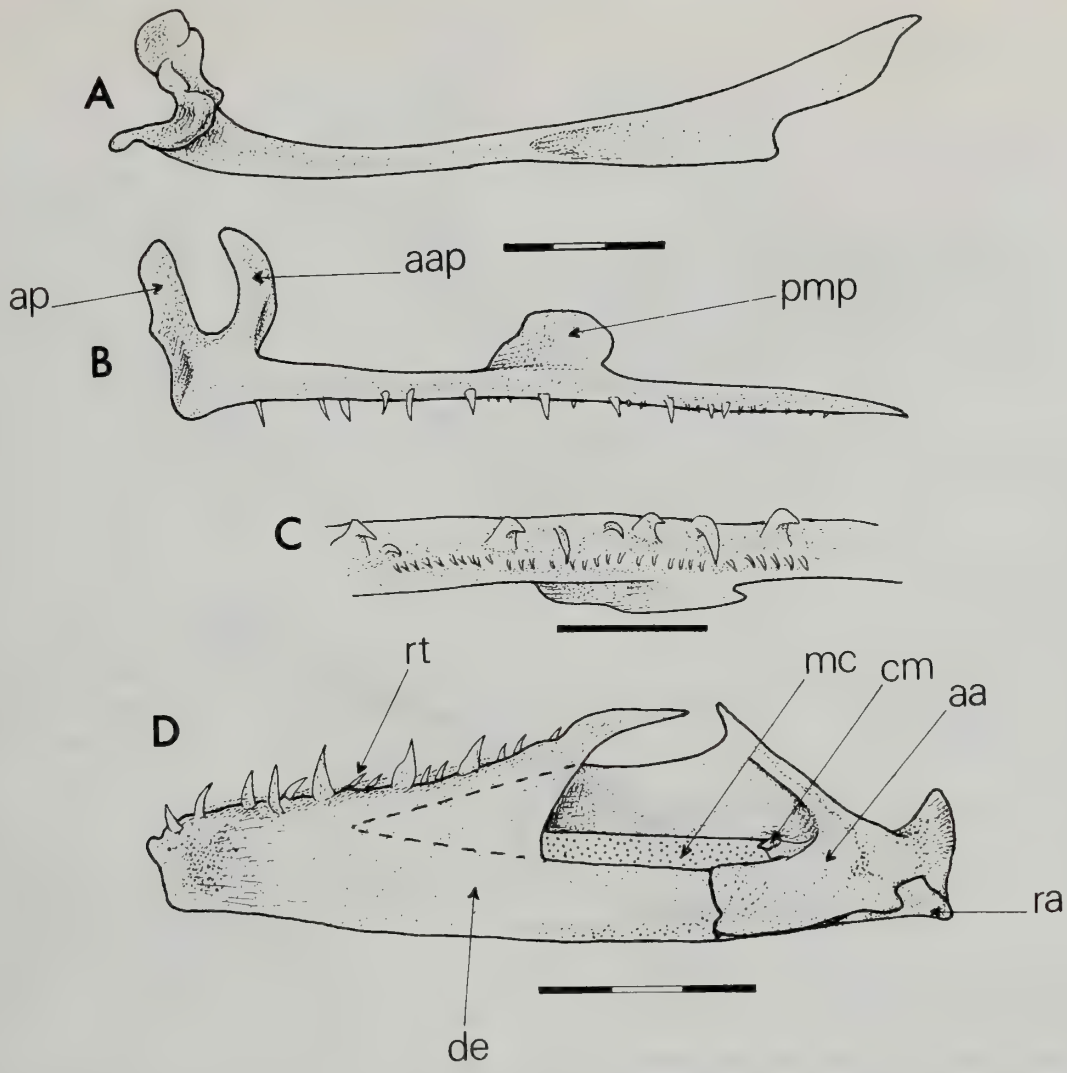

Fig. 11 *Macruronus magellanicus*, jaw bones. A, maxilla in dorsal view; B, premaxilla in lateral view; C, ventral view of the region of the premaxilla below the postmaxillary process showing double row of teeth; D, medial view of the lower jaw. A-C, BMNH 1936.8.26: 352–7 (skeleton); D, 1936.8.26: 342–56 (alcian-alizarin stained preparation).

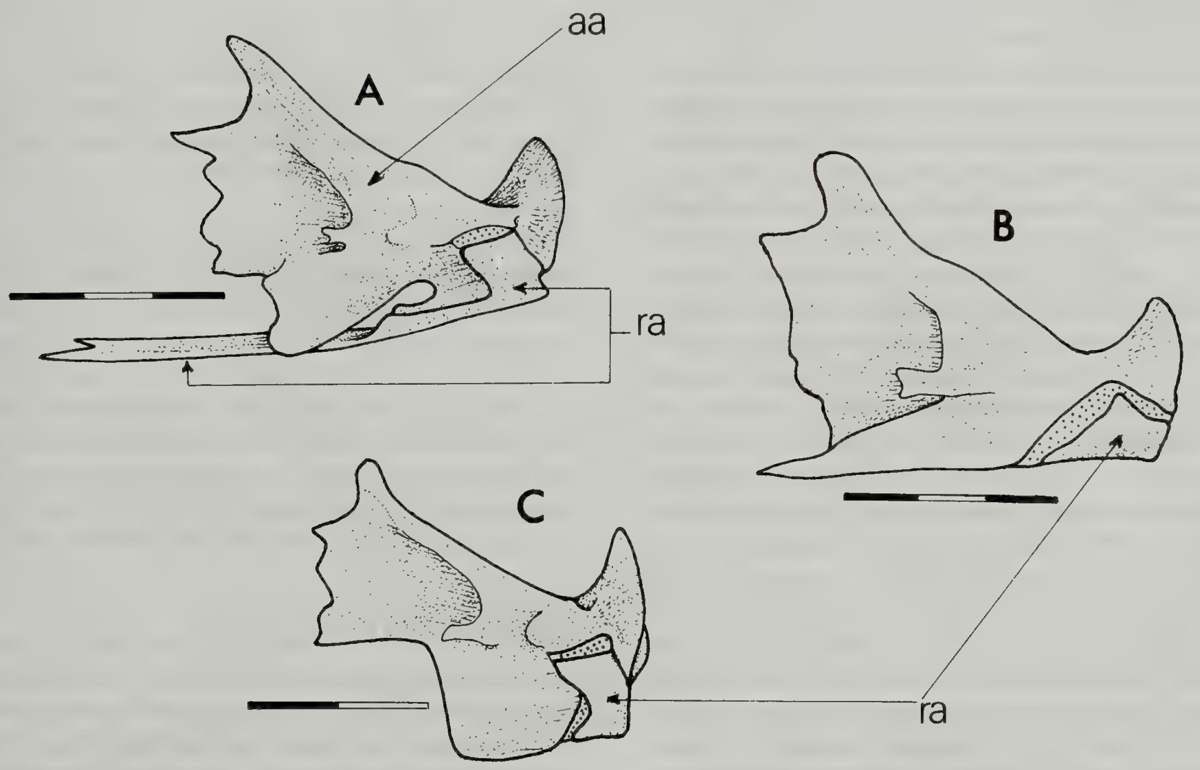

Fig. 12 Posterior region of the lower jaws, in medial views of; A, *Macruronus magellanicus* (BMNH 1936.8.26: 342–56); B, *Merluccius merluccius* (1971.7.21: 44–57); C, *Steindachneria argentea* (1963.2.25: 344–54). All alcian-alizarin stained preparations (the coronomeckelian cartilage has been omitted).

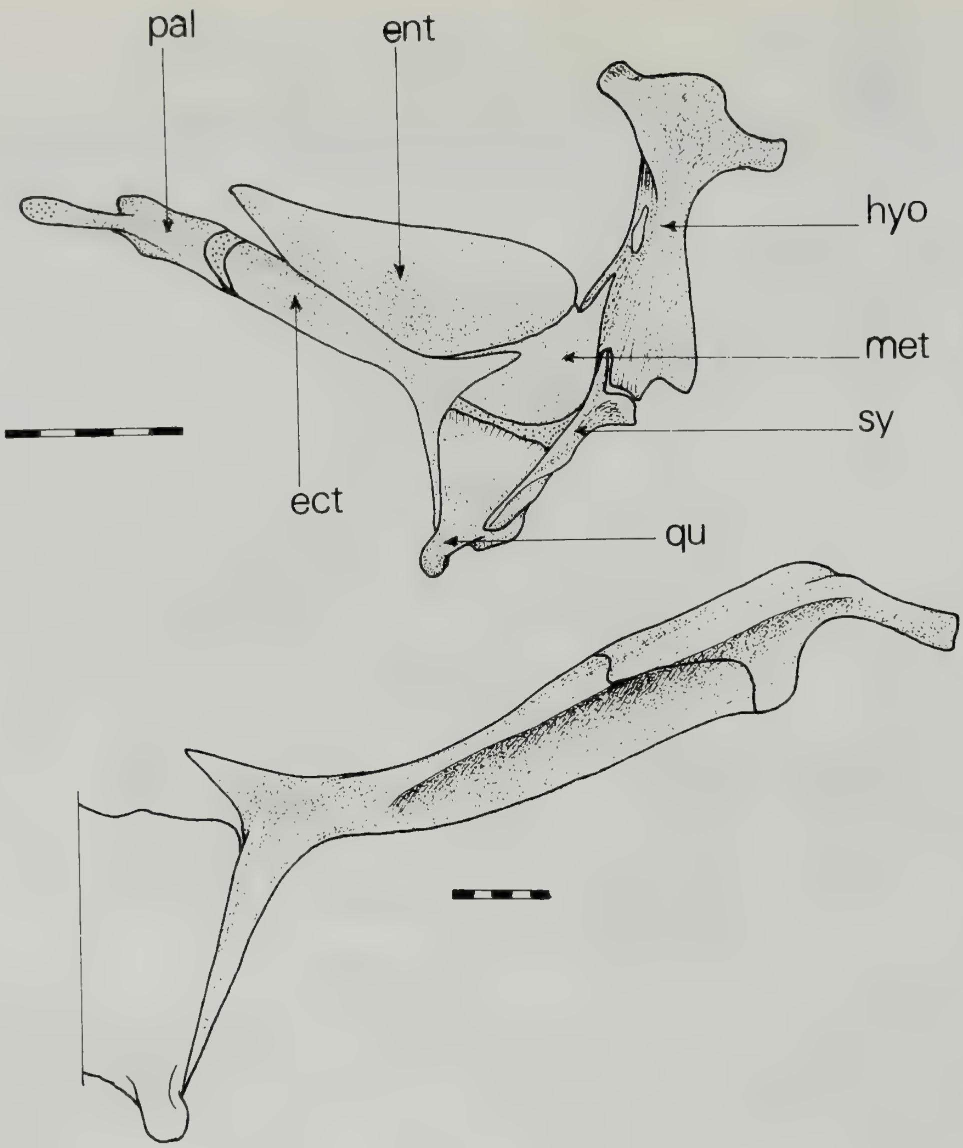

Fig. 13 *Macruronus magellanicus*, suspensorium and palato-pterygoid series. Above, medial aspect (BMNH 1936.8.26: 342–56, alcian-alizarin stained preparation); below, lateral view of palatine and ectopterygoid (1936.8.26: 358–63, skeleton).

The suspensorial elements of *Merluccius* differ in several respects from those of *Macruronus*: Palatine is deeper posteriorly, bearing a shallow lateral depression for the origin of *adductor mandibulae* A1b; ectopterygoid not extending as far ventrally along quadrate border and not posteriorly forked; entopterygoid not as extensive nor meeting metapterygoid (Inada, 1981:76); symplectic short and oblong; metapterygoid's posterior border extends further dorsally along hyomandibular limb; hyomandibular has deep cranial articulatory and long opercular processes. The most notable feature of the *Merluccius* hyomandibular, lacking in *Macruronus*, is a broad, lateral flange bearing two ventrally directed processes (Fig. 14A). Inada (1981) found significant enough differences in the size of the anterior (intermuscular) process to recognise two species groups of *Merluccius*.

Opercular bones

Macruronus (Fig. 15A) has a deep *interopercular* with an extended anterior tip; dorsomedially is a shallow articular facet with which articulates the interhyal; posterior border vertical. Extensively broad ligament joins interopercular to medial face of preopercular. *Preopercular* deep with long upright part, medially bearing a pronounced process which articulates with symplectic cartilage. *Opercular* broadly triangular with a well-developed horizontal medial ridge. *Subopercular* broadly triangular with rounded borders contacting opercular and preopercular, overlapped extensively by latter. An interopercular-subopercular ligament is absent.

Merluccius differs most noticeably from *Macruronus* in interopercular morphology (Figs 15B & 16C). The bone's anterior tip is blunter, its posterior border subtriangular and extended; dorsomedial articular surface highly developed with a thick rim acting as a stop to the posterior movement of the interhyal. Interopercular-preopercular ligament narrow, also a narrow interopercular-subopercular ligament. Subopercular oblong with straight posterior border contacting opercular with only narrow portion of anterior margin being overlapped by preopercular. Opercular with strong medial ridge.

Hyoid arches (Fig. 16A)

There are only minor differences between the hyoid bar elements of *Macruronus* and *Merluccius*. In *Macruronus* *anterohyal* deeper and shorter but *posterohyal* somewhat longer than in *Merluccius*. Two last *branchiostegal rays* of *Macruronus* more expanded and spathiform than those of *Merluccius* (Fig. 16C); in both genera the posterohyal supports one branchiostegal.

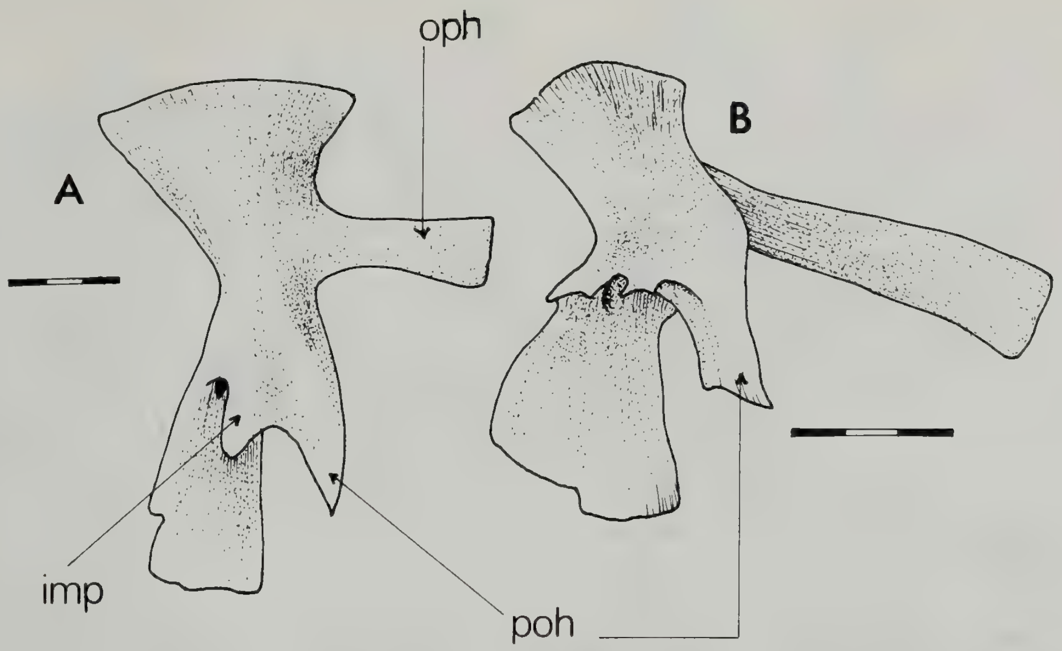

Fig. 14 Hyomandibular, in lateral views of A, *Merluccius productus* (BMNH 1896.9.25: 6) and B, *Microgadus proximus* (1890.11.15: 237), to show lateral shelf, discussed on p. 101.

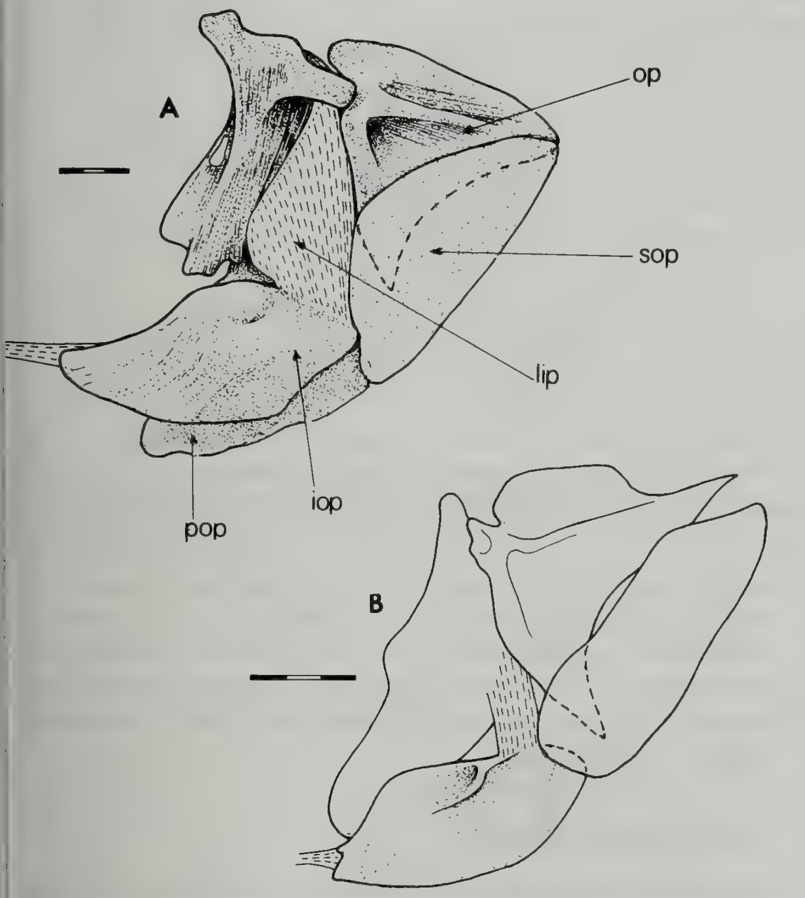

Fig. 15 Opercular series, medial views of A, *Macruronus magellanicus* (BMNH 1936.8.26: 342–56); B, *Merluccius merluccius* (1976.8.30: 87–96), alcian-alizarin stained preparations.

Urohyal is significantly different in the two taxa; that in *Macruronus* has an extended, rod-shaped anterodorsal (basibranchial) process (Fig. 16B). The basibranchial process of *Merluccius* urohyal is a fan-shaped plate (Fig. 16C) which more closely resembles urohyal shape of other gadoids; in other gadoid taxa, however, the urohyal basibranchial process is merely a continuation of the vertical median plate or keel of the bone and is not distinctly separated as in *Merluccius* (see Fig. 16C, also Inada, 1981, fig. 36, *cf.* Kusaka, 1974, figs 176–184 of various gadoids including *Macruronus*).

Branchial arch

Macruronus differs from *Merluccius* in several respects in the lower branchial arch elements (Fig. 17).

Macruronus has three median elements, an elongate, dumbell-shaped *basihyal*, a small cartilaginous 1st *basibranchial* articulating with the 2nd hypobranchials, an elongate, ossified 2nd basibranchial articulating with 3rd hypobranchials, and a minute, cartilaginous 3rd basibranchial lying at posterior tip of 2nd basibranchial. Between 4th ceratobranchials a tough ligament stretches from 3rd basibranchial, bifurcates and attaches to both 5th ceratobranchials. The 3rd hypobranchial is elongate with ventrally curved medial border; posteriorly it articulates with both 3rd and 4th ceratobranchials, both bearing elongate tooth-plates.

Merluccius has a relatively short rod-shaped basihyal, a long cartilaginous basibranchial articulating with 1st and 2nd hypobranchials and a short, arrow-head shaped basibranchial articulating with broadly triangular 3rd hypobranchials (Inada, 1981).

Macruronus has 9 long, denticulate *gill-rakers* on 1st hypobranchial, *Merluccius* has 3–10 small, denticulate tubercular rakers. Both genera have elongate *cerato-* and *hypobranchials*, the outer ceratobranchials of *Macruronus* bearing 14–15 rakers, those of *Merluccius* 11–12. Like other gadoids, *Macruronus* has two rows of rakers on all arches, those on inner surfaces of 1st and outer and inner surfaces of 2nd–4th hypo- and ceratobranchials, short, flat and spinose; those on inner margins of the elements transversely arranged, with their broadest face directed anteriorly (Fig. 18A). In *Merluccius*, gill-rakers on inner side of 1st arch and subsequent arches are small, tubercular and spinose but arranged so their broadest face is directed along ceratobranchial axis; below and surrounding the base of each raker may be one to six small denticulate patches (Fig. 18B; Inada, 1981, figs 47 & 48).

Upper branchial elements in *Macruronus* comprise four rather short *epibranchials*, all with tall, uncinate processes

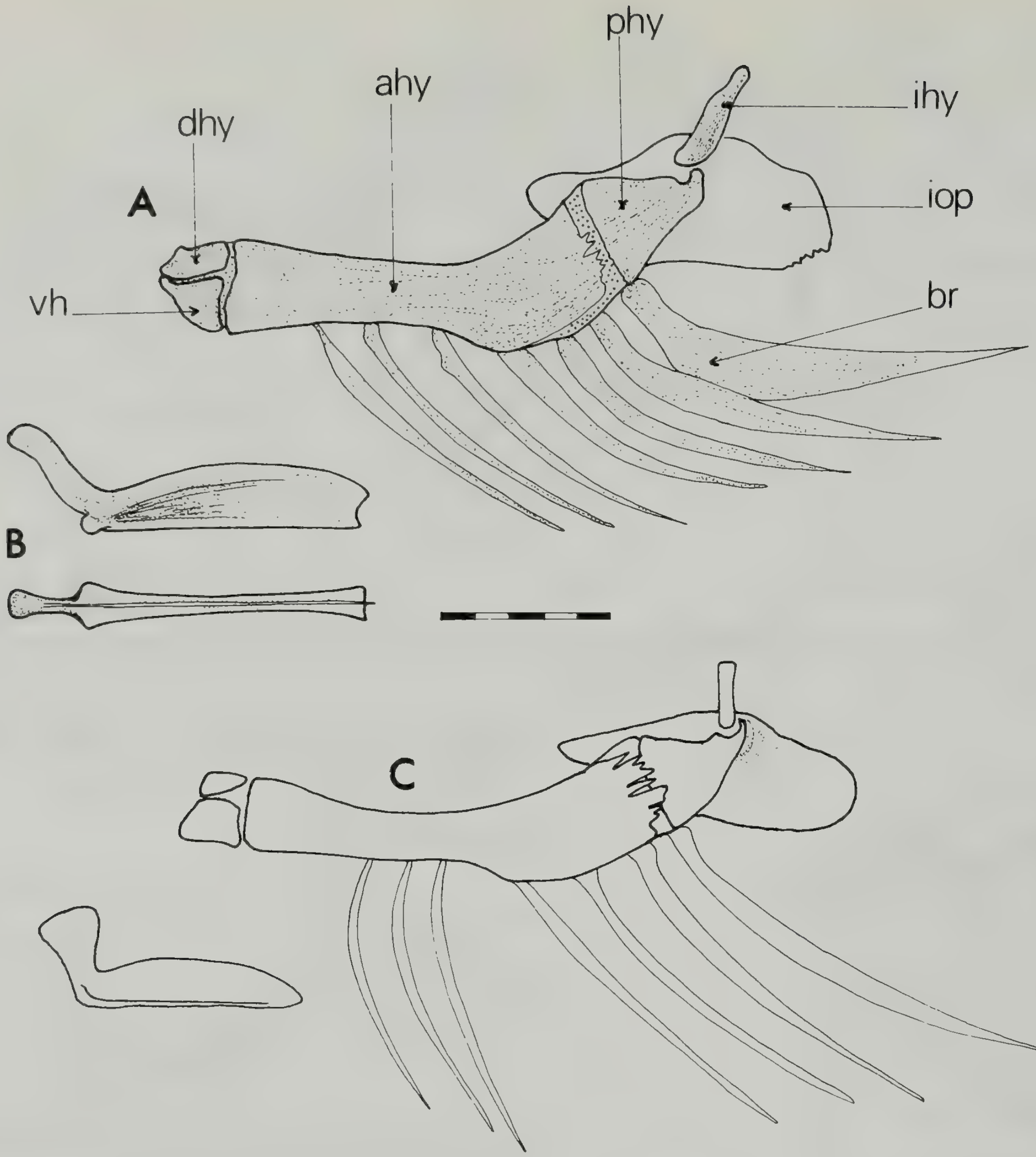

Fig. 16 Hyoid arch elements of; A & B, *Macruronus magellanicus* (BMNH 1936.8.26: 342–56), and C, *Merluccius merluccius* (1971.7.21: 44–47), alcian-alizarin stained preparations. The hyoid bar in A is shown in medial view, the urohyal in B & C in lateral and (B) dorsal views.

and three *pharyngobranchials* (numbers 1–3). Pharyngobranchial 1 is cartilaginous; pharyngobranchial 3 bears three struts which articulate with the 2nd, 3rd and 4th epibranchials; pharyngo-branchial 2 articulates with the 1st epibranchial; *interarcual cartilage* absent. There are 8 slender, denticulate gill-rakers on outer surface of 1st epibranchial and 2 or 3 flat, denticulate rakers on inner surface. Similar rakers occur on 3rd and 4th epibranchials. Tooth patches are present on 3rd epibranchial and pharyngobranchials 2 and 3.

In *Merluccius* epibranchial uncinate processes are lower than in *Macruronus* and the struts of pharyngobranchial 3 are longer and prominently curved mesad. Inada (1981) and Patterson & Rosen (1989) report pharyngobranchial 1, but there is no interarcual cartilage. Tooth patches are present on pharyngobranchial 2 and 3 and on 3rd epibranchial. Epibranchial 1 bears 0–3 long gill-rakers on outer margin and two or three short, cylindrical denticulate rakers along inner surface.

Pectoral girdle (Fig. 19)

Principal differences between pectoral girdle elements of *Macruronus* and *Merluccius* are in the *cleithrum*, which in the former lacks the prominent dorsoposterior process of the latter (Inada, 1981:85; fig. 38); *coracoid*, which in *Macruronus* has a relatively short anteroventral process; and *postcleithrum*, which is longer and more deeply curved than in *Merluccius* with an arrow- as opposed to a club-shaped head (Inada, 1981; figs 39, 40).

Pelvic girdle (Fig. 20)

Noticeable differences occur in *pelvic bone* shape between *Macruronus* and *Merluccius*. In *Macruronus*, pelvic bone elongate with strongly developed lateral lamina; postpelvic process long and ventroposteriorly curved, articular surface for the fin rays short. In *Merluccius* pelvic bone broad with wide medial horizontal lamina and low lateral ridge; postpelvic process long but straight, articular surface for fin rays extensive. *Macruronus* with 8 pelvic rays, *Merluccius* with 7.

Gosline (1963:12) noted that in *Microgadus* (Gadidae) the pelvic girdle has a medial projection which overlaps and ligamentously joins its partner, further remarking on the absence of 'such projections' in *Merluccius*. Rosen & Patterson (1969:432) take up Gosline's remark in referring to the pelvic bones of the fossil *Rhinocephalus* by stating that

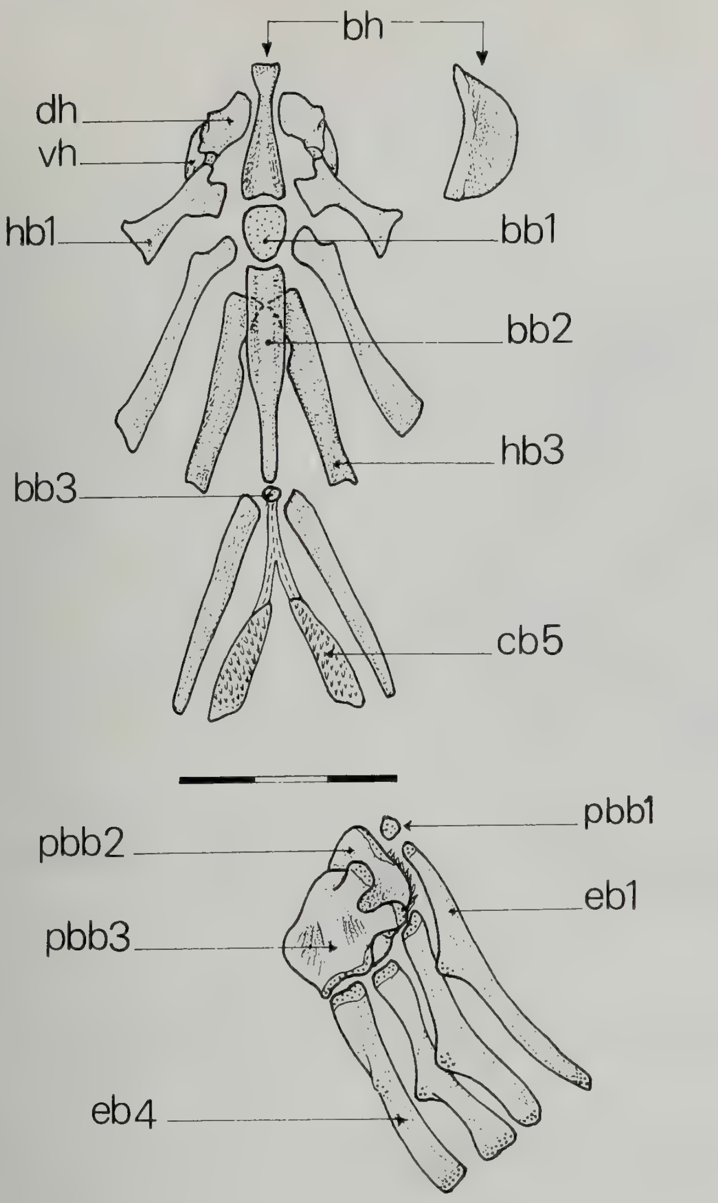

Fig. 17 *Macruronus magellanicus*, branchial arches. Above, lower elements in dorsal view; the basihyal is also shown in lateral view. Below, upper elements, right side, in dorsal view. Coarse stippling= cartilage. Alcian-alizarin stained preparation, (BMNH 1936.8.26: 342–51).

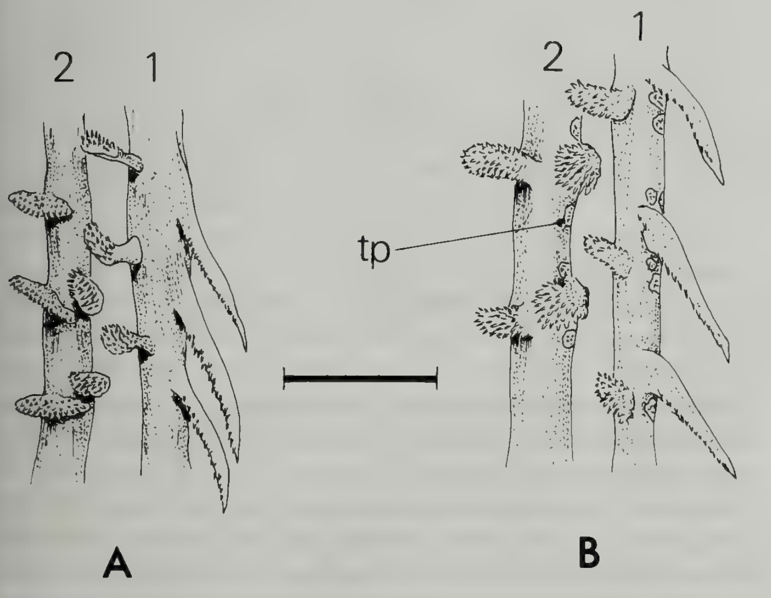

Fig. 18 Gill-rakers on the outer (1) and second (2) ceratobranchials of A, *Macruronus magellanicus* (BMNH 1936.8.26: 342–351); B, *Merluccius merluccius* (1971.7.21: 44–47; alcian-alizarin stained preparations).

this taxon resembles gadids and macrourids and '... not that of merlucciids, in having medial processes'. Fahay (1989) in describing the pelvic girdle of *Steindachneria* takes this statement a stage further by remarking that the postpelvic processes are reduced and the pelvic bones meet *via* medial processes. He likens *Merluccius* and macrouroids where '... the posterior arms are directed posteriorly'. None of these statements is strictly correct, however. The so-called median processes of some gadids (*Gadus*, *Microgadus*, *Merlangius*) appear to be only an extension of the lamina anterior to the postpelvic process; the processes themselves still point posteriorly as is indicated by the pronounced ridges of bone which mark their position. Okamura (1970) considered the postpelvic process of several macrouroids to have been reorientated transversely.

Fahay's (1989) illustration of the pelvic girdle of *Steindachneria* shows that it differs little from that of *Bathygadus* (Howes & Crimmen, 1990, fig. 24), except that its postpelvic processes are angled somewhat anteriorly and as such I would interpret the pelvic girdle of *Steindachneria* as being plesiomorphic. On the other hand, the development of extensive laminae joining in the midline appears to be synapomorphic for the Gadidae, at least in those genera examined, *Gadus*, *Merlangius*, *Trisopterus*, *Melanogrammus*, *Theragra*, *Microgadus*.

Vertebral column (Fig. 21)

Macruronus magellanicus has 19–21 *abdominal vertebrae* (those, apart from the first four, bearing short, broad parapophyses) and 57–59 *caudal vertebrae* (those bearing a haemal spine; Fahay & Markle, 1984 give 58–60 for *M.novaezelandiae*); first four vertebrae are shorter than others, 2nd markedly compressed, only half the length of 5th. Prezygapophyses of 1st centrum ligamentously attached to compressed condyles of exoccipital; Baudelot's ligament attaches to lateral cavity of 1st centrum (see below). Third and 4th vertebrae each bear pair of ribs and epipleural ribs attach to tips of parapophyses of the other abdominal vertebrae.

Merluccius has 21–29 abdominal and 24–31 caudal vertebrae (Fahay & Markle, 1984). The abdominal elements bear extensive, wing-like parapophyses which become successively broader at the 11th or 12th vertebrae then diminish in size. Three or four pairs of ribs borne by 3rd-5th or 6th vertebrae (Inada, 1981:89).

Baudelot's ligament (Fig. 22) In *Macruronus* Baudelot's ligament thick, stretching from lateral cavity of 1st centrum, passing through head kidney and attaching laterally and complexly to pectoral girdle; the ligament shares an aponeurosis with postero- and anterolateral segments of epaxial muscle; it then divides into two broad bands one of which attaches to posteromedial rim of supracleithrum, the other to dorsomedial surface of cleithrum. In *Merluccius*, Baudelot's ligament is thin, running from 1st centrum; although divided and attached to both cleithral elements it does not join with any muscle segment.

Dorsal and anal fins. *Macruronus* has two dorsal fins. *First dorsal* comprises a minute first ray and 13 long, segmented rays all of which are supported by long, broad distal radials. *Second dorsal* confluent with caudal fin, has 90–92 rays supported by slim radials. *Anal fin* has 83 rays, the anterior six to eight produced, giving lunate border to anterior margin of fin.

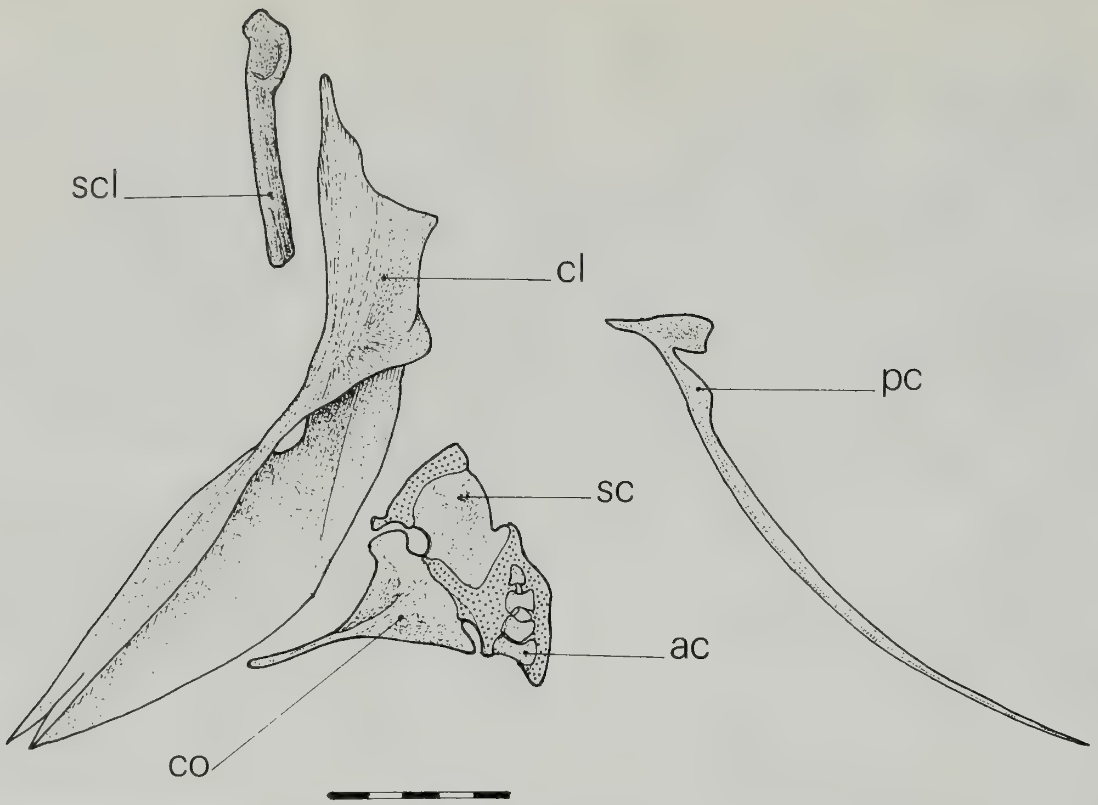

Fig. 19 *Macruronus magellanicus*, pectoral girdle in medial view. For clarity the coracoid, scapular and postcleithrum have been separated from the cleithrum (BMNH 1936.8.26: 342–351, alcian-alizarin stained preparation).

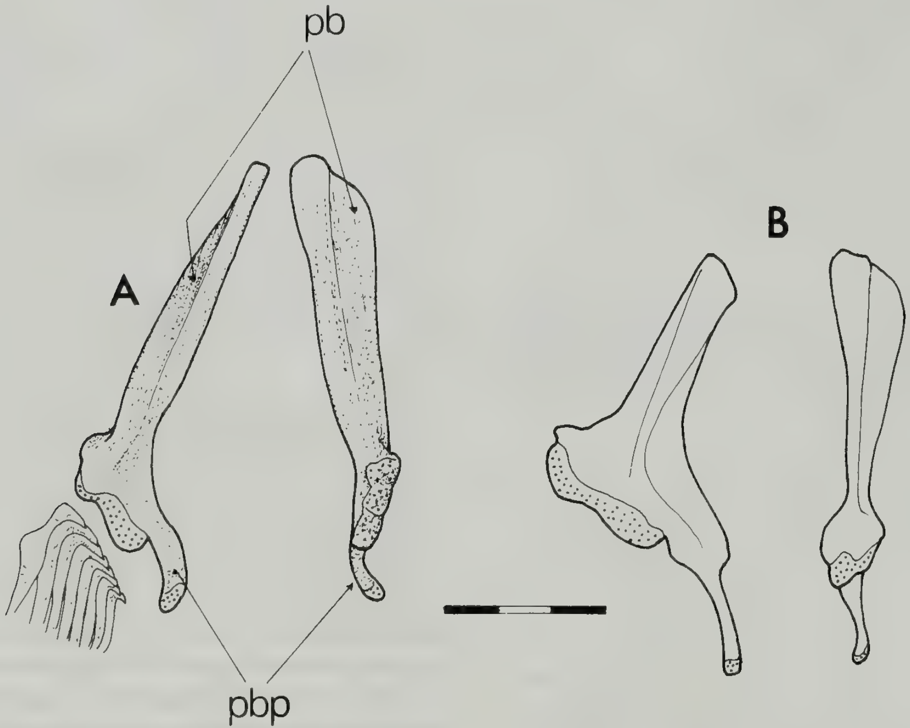

Fig. 20 Pelvic bone in dorsal (left) and lateral (right) views of; A, *Macruronus magellanicus* (BMNH 1935.8.26: 342–351) and B, *Merluccius merluccius* (1971.7.21: 44–49, alcian-alizarin stained preparations).

Merluccius has two dorsal fins. First dorsal 8–13 rays, second dorsal with 34–45; middle rays of second fin shorter than others, giving fin a notched appearance. Anal fin has 35–46 rays, also notched, anterior rays not produced. Dorsal and anal fins widely separated from caudal fin origin.

Principal differences in the vertebral column between *Macruronus* and *Merluccius* lie in the extreme development, in the latter, of the abdominal parapophyses which form a dorsal covering to the swimbladder, the lateral wall of which is firmly attached to the parapophyses. In *Macruronus* the swimbladder is a cigar-shaped structure with an anterior bifurcation, and lacking intimate attachment to the parapophyses (Fig. 21).

In both genera the first radial of the first dorsal fin lies between 2nd and 3rd neural spines (Fig. 21). The neural spines and fin radials of *Macruronus* are thinner and larger than those of *Merluccius* and the dorsal laminae of the prezygapophyses taller. Although both genera have nearly equal numbers of abdominal vertebrae, *Macruronus* has more than twice as many caudal vertebrae, making a total

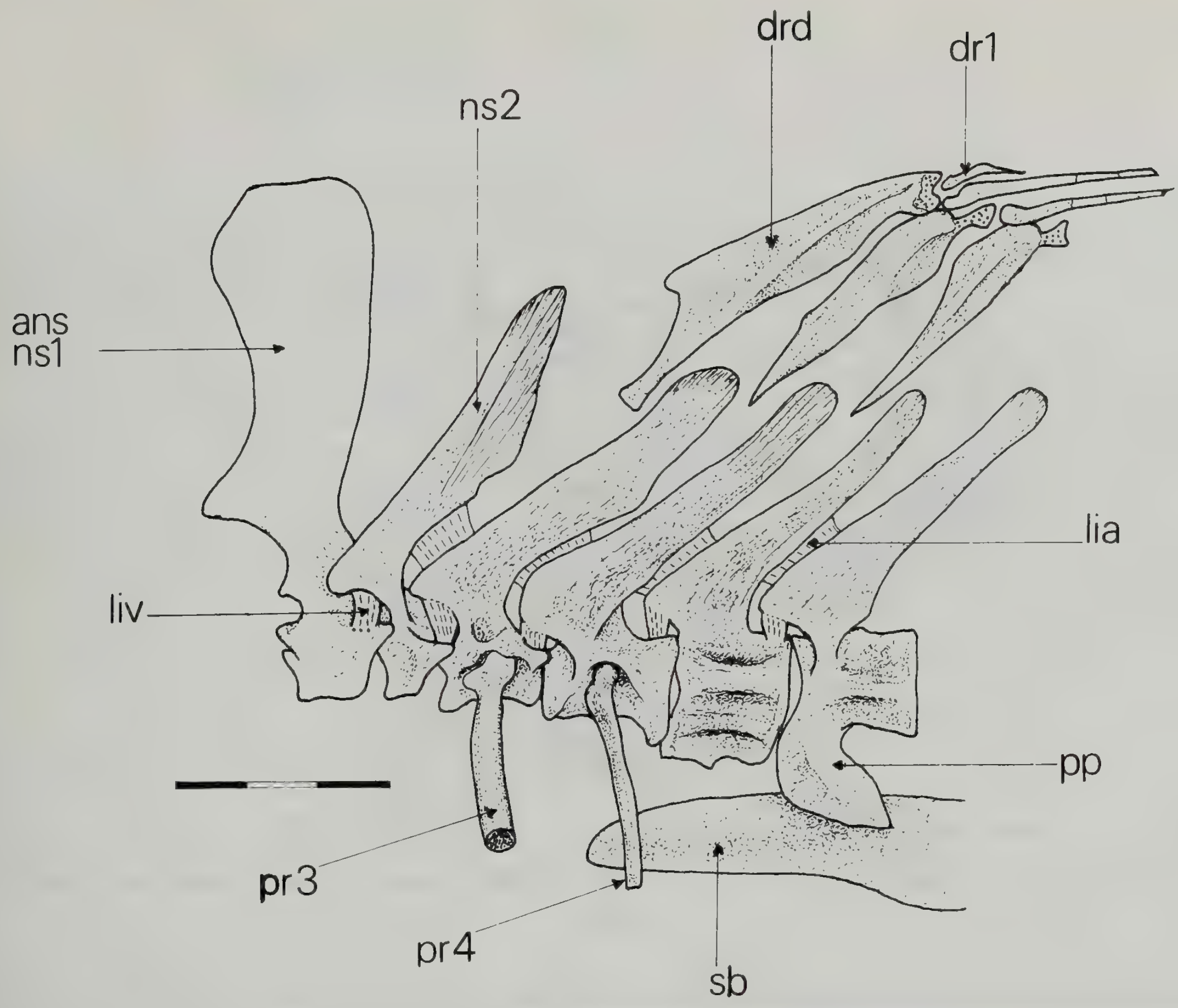

Fig. 21 *Macruronus magellanicus*, vertebral column and dorsal fin supports in lateral view. Drawn from dissection of BMNH 1936.8.26: 342–351, supplemented by radiographs.

difference of *ca* 20. There are nearly three times as many second dorsal fin rays and twice the number of anal rays in *Macruronus* than *Merluccius*.

Caudal fin skeleton (Fig. 23)

In *Macruronus* eight elements bear caudal fin rays *viz*, rays having a simple, rounded articulatory head as distinct from anvil or hammer shaped heads of dorsal and anal rays. Three vertebrae (terminal; two preural) are involved directly or indirectly with the caudal rays. Last centrum posteriorly compressed and upturned, having the appearance of a hypural plate to which attach four fin rays. Terminal centrum is assumed to be second ural centrum plus fused 3rd–5th hypurals, and possibly a uroneural. The penultimate vertebrae (assumed to be 1st preural plus 1st ural) is associated with four, posteriorly directed rod-like elements none of which is fused to the centrum. The two ventral elements have cartilaginous proximal and distal tips and each support fin rays. These appear to be the parhypural (anterior element) and fused 1st and 2nd hypurals (posterior element). Both bones articulate with deeply concave ventral surface of the centrum and lie adnate to one another and to the vertebral surface. The two dorsal elements have expanded proximal surfaces which interlock with one another and articulate with the dorsal surface of the centrum. The posterior of these two elements has broad lateral flanges; each element bears a caudal ray and are identified as epurals. The 2nd preural vertebra bears distinct neural and haemal spines, each of which appears to incorporate a radial. The dorsal 'radial' lies adnate to the posterior surface of the neural spine leaving a small space between its proximal tip and the vertebral surface. The ventral element is basally co-ossifed with the haemal spine but it does not extend to the base of the spine; the haemal arch is greatly reduced but is nontheless present. Both dorsal and ventral 'radials' bear caudal rays. The 3rd preural centrum bears long, low-angled, neural and haemal spines each preceded by a long radial; the ventral radial bears what appears to be a caudal fin ray, but the dorsal radial articulates with a dorsal fin ray. Both dorsal and ventral radials bear anterior and posterior flanges, the anterior of which articulates with the head of the preceding radial.

The caudal fin skeleton of *Merluccius* is also symmetrical, the hypural plate supports 5 or 6 fin rays (Fig. 24). Combined 1st and 2nd hypurals articulate with 1st preural centrum and bear three fin rays. A parhypural lies between the lower hypural plate and the haemal spine of the 2nd preural vertebra and bears a single fin ray. Dorsally, two epurals, each bearing a fin ray, lie above 1st ural centrum; 2nd preural centrum bears compressed neural spine which supports single fin ray. Lying between the neural and haemal spines of 2nd and 3rd preural vertebrae are, respectively, X and Y bones, each bearing a fin ray.

Dorsal and ventral accessory bones, usually termed X and Y bones are lacking in *Macruronus*. Markle (1982) noted that X and Y bones can readily be distinguished from other autogenous elements because they have cartilaginous articulating surfaces. However, such a distinction only applies in small, incompletely ossified specimens; in adults of

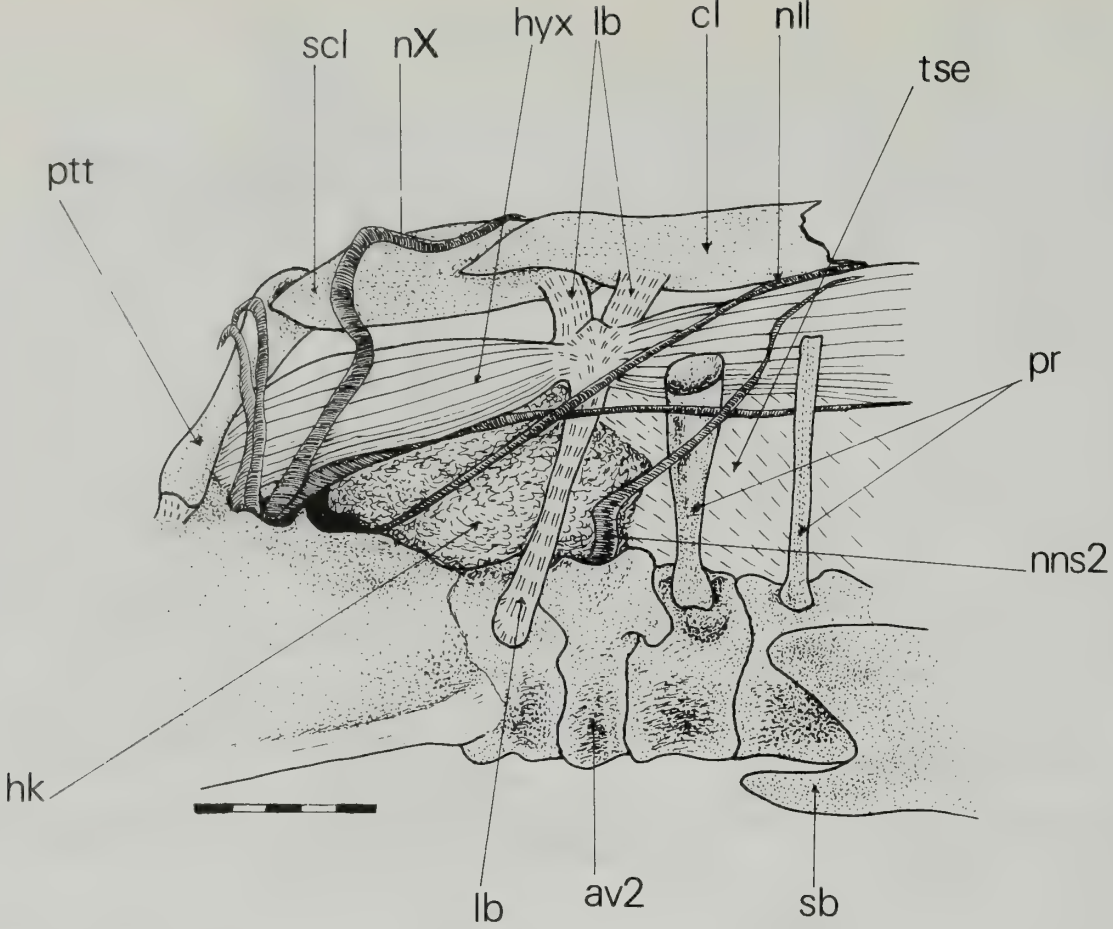

Fig. 22 *Macruronus magellanicus*, anterior part of the vertebral column and pectoral girdle in ventrolateral view showing the attachments of Baudelot's ligament (same specimen as in previous figure).

Merluccius X and Y bones are fully ossified. Besides, in partially ossified specimens the articulating surfaces of all autogenous elements are cartilaginous. The identity of X and Y bones is determined by their position, which is always between the second and third preural neural and haemal spines.

Like Markle (1982) I find 'extra' or bifurcate neural and/or haemal spines on PU2 (Markle's PU1). I have found in *Merluccius* the development of extra neural and haemal spines on the second preural vertebra. In one specimen (Fig. 25A) the posterior neural spine appears to be a composite element, *viz* the spine plus a co-ossified radial; thus resembling the situation in *Macruronus* (see above). In a second specimen (Fig. 25B) a single, short, spine-like process extends from the base of the neural spine to stand between the spine and the X bone. In a specimen of *Gadus morhua* (Fig. 26) the neural and haemal spines of the second preural vertebrae are clearly composite elements. The halves of the neural and haemal spines grip lamellate elements (probably the X and Y bones), that associated with the haemal spine being contiguous with the parhypural.

Fahay & Markle (1984) have suggested that the aquisition of X and Y bones and modifications of the posterior preural neural and haemal spines were necessary precursors of the gadoid symmetrical tail fin.

Caudal fin muscles (Fig. 27)

In *Macruronus* there are two thin and narrow superficial layers of longitudinal muscles running dorsally and ventrally along the posterior part of the vertebral column. These muscle bands are continuous anteriorly with the epaxial and hypaxial musculature; they insert *via* thin tendons respectively to the upper (third) and lower (fifth) 'caudal' rays. Since these muscle bands have no attachments to the neural and haemal spines or to the lateral surfaces of the centra, other than by loose connective tissue, I regard them, as respectively, epaxial and hypaxial muscles. Their insertion to the caudal rays is not unlike that of the epaxial and hypaxial muscles in other teleosts (eg.*Elops*, shown in Winterbottom, 1974, fig. 48). If the insertions of the hypaxial and epaxial muscle bands should be the criteria defining a caudal ray, then the number of rays would be 7 rather than 11 as given above (cf. Figs 23 & 27A). The deeper dorsal muscle layer runs posterodorsally from the supporting radials to insert on the bases of the upper caudal rays. There are two components of these muscles, one running to the shaft of the ray, the other passing mesad to the base of the ray. The fibres originating from the terminal centrum are clearly differentiated into a separate segment (hsh, Fig. 27A). Those anteriorly, however, become continuous with and indistinguishable from, the *erectores* and *depressores dorsales* of the dorsal fin rays. The deeper ventral muscle layer is similarly arranged to the dorsal, except that there is no terminally differentiated bundle; the series running from the ventro lateral cavities of the centra and the supporting radials to insert on the ventral caudal rays. Long, narrow bundles of fibres ('*interradialis*') connect the caudal rays with one another. The central caudal fin ray is identified as such by the angle of the '*interradialis*' fibres connecting it with the immediate upper and lower rays, *viz* posterodorsally or posteroventrally (Fig. 27A).

The caudal fin musculature of *Merluccius* is essentially

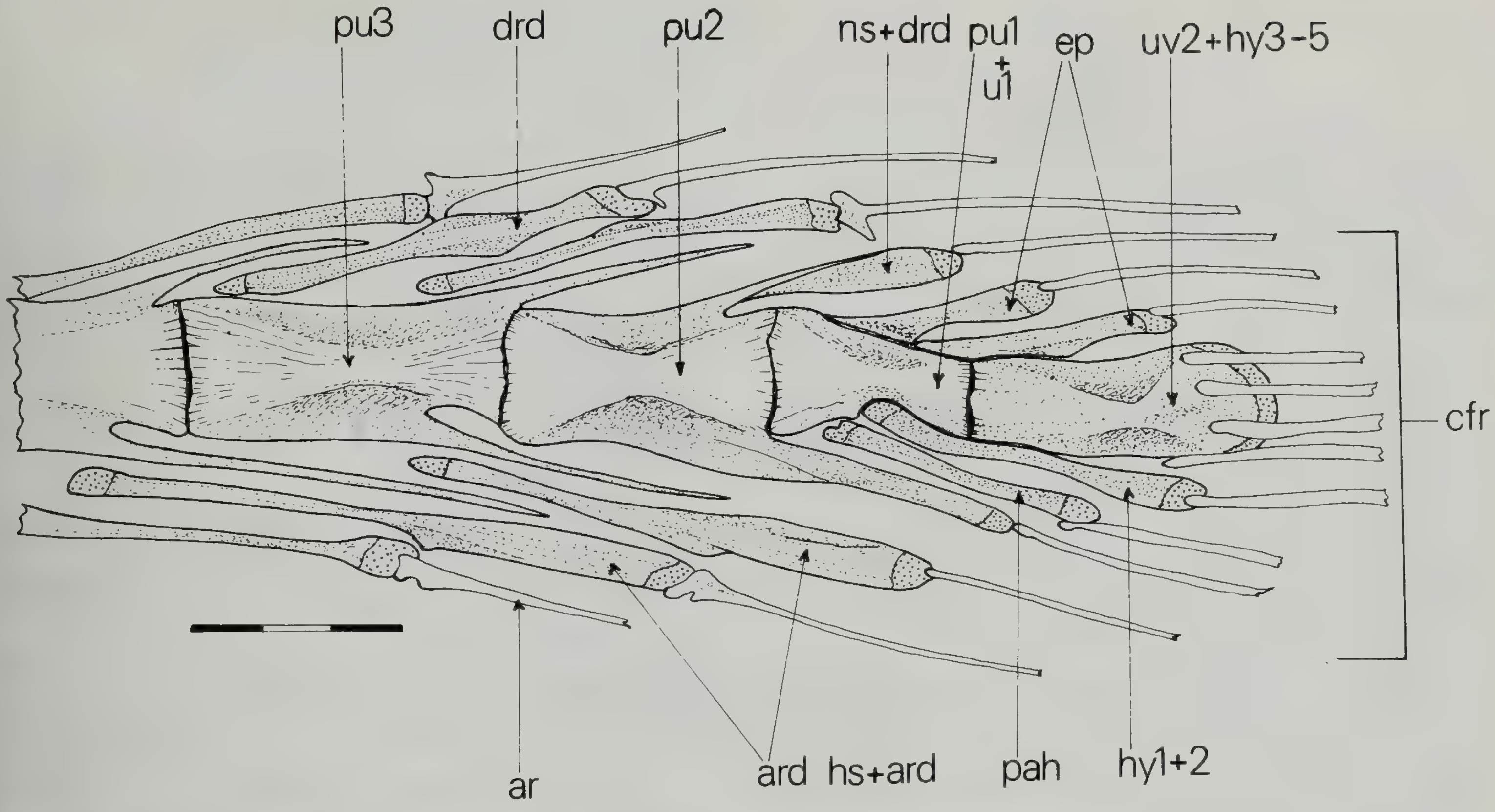

Fig. 23 *Macruronus magellanicus*, caudal fin skeleton (BMNH 1936.8.26: 358–63, alcian-alizarin stained preparation of tail region).

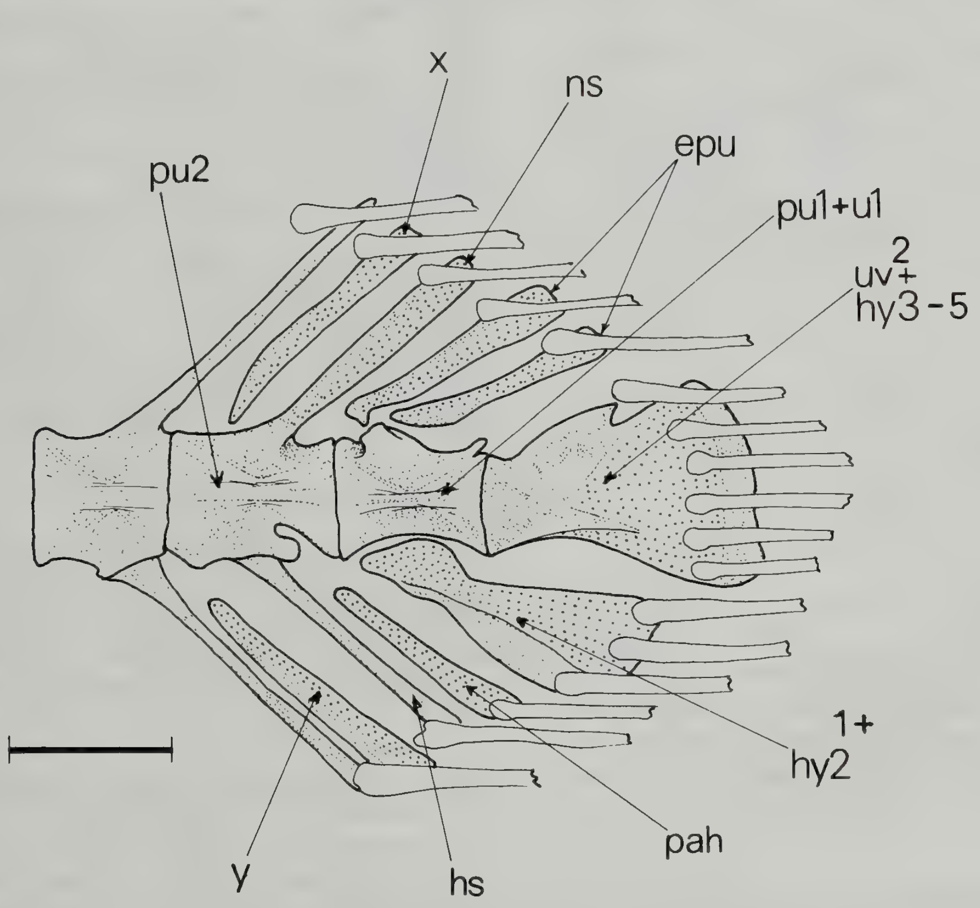

Fig. 24 *Merluccius merluccius*, caudal fin skeleton (BMNH 1976. 8.30: 87–96, alcian-alizarin stained preparation).

similar to that of *Macruronus*, as indeed it is in other gadoids examined. In *Gadus* the two component muscle insertions to the base of the caudal rays is clearly marked and appears no different from the arrangement of *depressores* and *erectores* muscle of the dorsal and anal fin rays. *Muraenolepis* exhibits a simplified system of caudal fin musculature in that no separate terminal segment arising from the hypural plate is differentiated. '*Interradialis*' muscles interconnect the posterior 22nd dorsal and 'caudal' rays and the posterior 18 anal rays (dorsal and anal ray numbers counted forward from the median caudal ray).

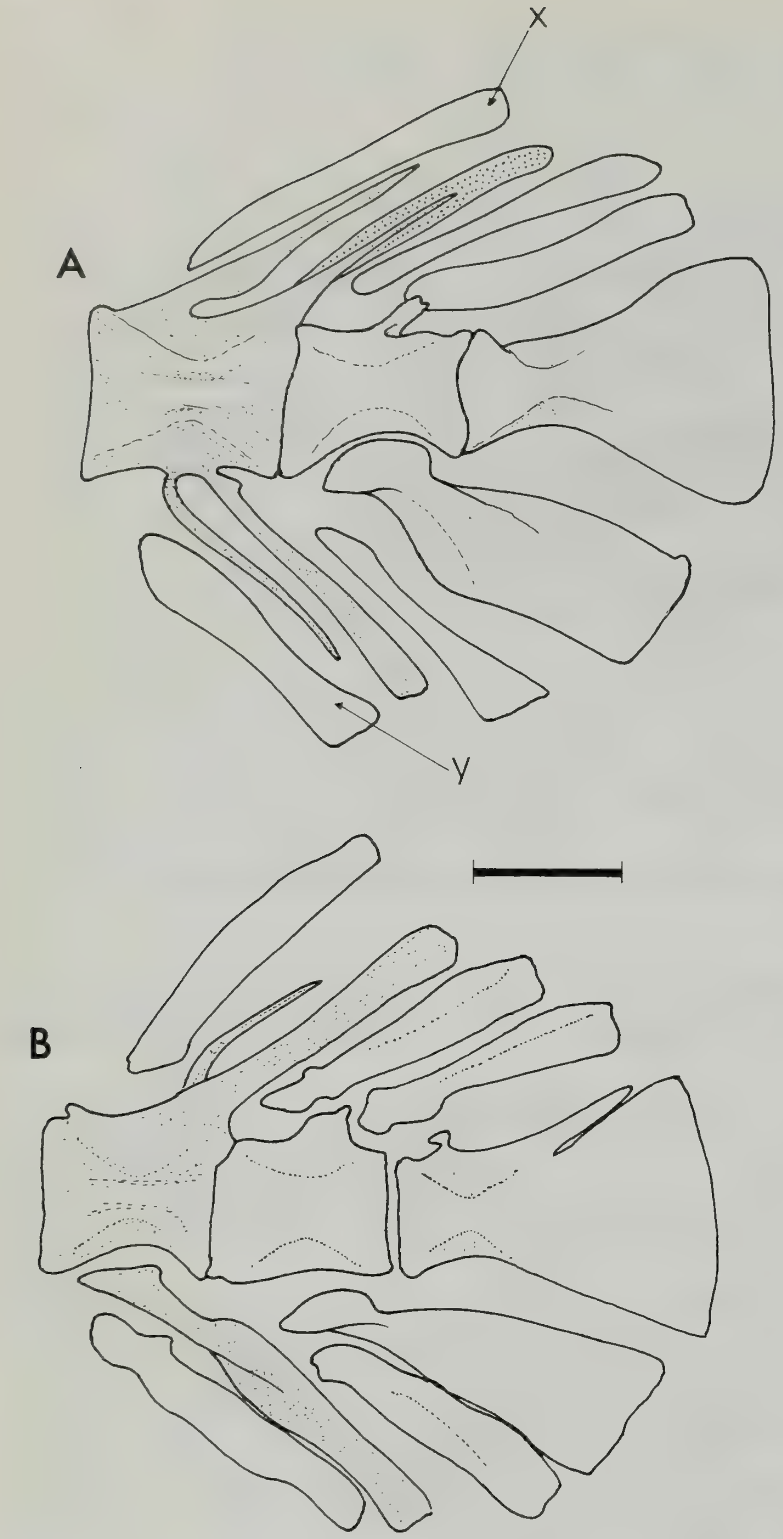

Fig. 25 Caudal fin skeletons of *Merluccius merluccius* in lateral views. Two specimens (ex. BMNH 1971.7.21: 44–59) showing individual differences (see text). Second preural vertebra and associated elements are shaded; cartilage is indicated by coarse stippling. Scale=1.0mm.

Epaxial muscle insertion (Fig. 26A)

In *Macruronus* epaxial musculature extends well forward to insert on the cranium above the posterior region of the orbit. Central section of the muscle bloc inserts along supraoccipital crest, its fibres forming an angle of 20° to it. Anterolaterally a separate muscle segment branches from main body, continues forward and inserts on the diagonal frontal ridge posterior and medial to orbit. Epaxial muscle covers dorsal posttemporal limb.

In *Merluccius epaxialis* inserts mostly along posterior border of dorsal posttemporal limb; medially it inserts on supraoccipital and frontal crests. A small ventrolateral segment passes forward beneath posttemporal limb to insert in posttemporal fossa (Fig. 26B).

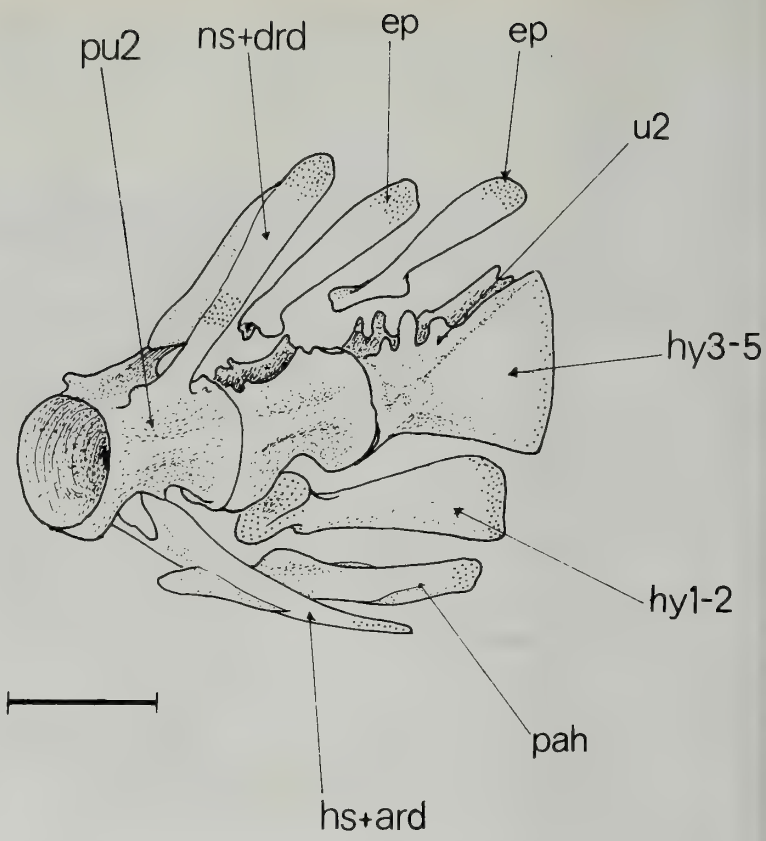

Fig. 26 Caudal fin skeleton of *Gadus morhua*, lateral aspect, viewed anterodorsally (ex. BMNH 1971.2.16: 628–33). Scale=0.5mm.

The *Merluccius* condition appears the more derived of the two. Among other gadoids it is usual for the *epaxialis* to insert along the posterior slope of the cranium; the medial fibres attach to the supraoccipital crest. In all other taxa examined the posttemporal limb is covered and the *ramus lateralis accessorius* (RLA) nerve passes lateral to the epaxial segment (Fig. 26C,E); RLA is absent in *Macruronus* and *Merluccius*.

Rectus communis muscle

Macruronus is unique in that the *rectus communis* muscle attaches, posteriorly, to the 5th ceratobranchial rather than, as in other gadoids, to 4th (Howes, 1988*a*:46). Anteriorly, the muscle attaches aponeurotically to the *sternohyoideus* as in the majority of other gadoid families (Howes, 1988*a*, table 2: 46).

Ramus lateralis accessorius (RLA) nerve

In most gadoids the recurrent branch of the facial nerve, RLA, leaves the cranium *via* a foramen in the parietal or between parietal and epioccipital. This foramen is absent in both *Macruronus* and *Merluccius*. Svetovidov (1948: 14) claimed that in *Merluccius* the foramen is covered by bony crests, but further (p. 133) remarks that parietal crests above the foramen are not developed; both statements are incorrect. Freihofer (1970) noted RLA as apparently absent in *Merluccius*. My observations confirm this absence.

Freihofer (1970) noted in *Merluccius* presence of accessory segmental lateral-line nerves serving the base of the pectoral fin. These also occur in *Macruronus*. Similar nerve patterns are reported by Freihofer (1970) to occur in a variety of paracanthopterygian, acanthopterygian and lower euteleostean taxa. This distribution suggests either a plesiomorphic or homoplastic presence (see discussion, p. 99)

Table 1. Comparison between *Macruronus*, *Merluccius* and other gadoids of characters discussed or noted in the text

Character	*Macruronus*	*Merluccius*	Other gadoids
Lateral ethmoid wing	flat	cone-shaped	cone-shaped in Gadidae, flat in others
Mesethmoid	gently sloped	acutely sloped	vertical in most, sloped in Melanonidae and Bathygadidae
Vomer	toothed	toothed	toothed; edentulous in Euclichthyidae and Bathygadidae
Nasal	narrow, trough-like	trough-like	various, broad in Bathygadidae
Cranial depth	deep	shallow	various, often shallow
Frontals	separate	separate	separate in most but fused in Gadidae and some Phycidae
Medial frontal crests	thick, enclosing central medial cavity	thin, no medial cavity	thin, variously developed or absent, enclosing anterior cavity in Gadidae
Frontal sensory canal	covered by broad roof	roof lacking	roof lacking
Frontal ventral lamina	converge	parallel	parallel (enclosed canal in Moridae)
Sphenotic border	indented	straight	straight
Prootic with medial projection	formed as a transverse wall	shelf-like	only in Gadidae
'Posterior myodome'	absent	present	absent
Parasphenoid	thin, round in cross-section	thick, flat in cross-section	variously developed usually thick and flat
Intercalar	forms posterior margin of lateral cranial wing	forms only part of posterior margin	forms posterior margin only in *Phycis* and *Muraenolepis*
Supraoccipital crest	low, embraced by 1st neural spine	high, embraced by 1st neural spine	variously developed usually only partly embraced by 1st neural spine
Exoccipital condyles	acutely sloped	gently sloped	usually horizontal
Posttemporal	covered by epaxial muscle, ventral limb long, in contact with posterior border of intercalar; dorsal and ventral limbs not in same vertical plane	exposed, ventral limb widely separated from intercalar, lies in same vertical plane as dorsal limb	covered by epaxial muscle, ventral limb separated from intercalar and pterotic margin, dorsal and ventral limbs not in same vertical plane
Extrascapulars	4, lateral	4, lateral and and medial	3 or 4, lateral and medial
Palatine contacts	mesethmoidal part of lat. ethmoid	mesethmoidal part of lat. ethmoid	mesethmoidal part of lat. ethmoid, except in Melanonidae, Bathygadidae and Steindachneriidae
Palatine origin of muscle A1Bβ	ventral cavity	lateral cavity	none
Retroarticular	anteriorly extended	short, triangular	short, triangular or L-shaped
Labial ligament attaches	anterior part of jaw	centre of jaw	usually centre but anteriorly in Bathygadidae and Melanonidae
Ento-and meta-pterygoid	in contact	widely separated	in contact
Hyomandibula flange	absent	with two ventrally directed processes	with a single ventrally directed process (only in 'higher' gadoids)
Suboperculum	broadly triangular	oblong	various, usually broadly triangular
Interopercular-posterohyal joint	absent	present	present only in in 'higher' gadoids
Interopercular posterior border	straight	rounded	rounded
Basihyal	elongate	short	short
1st pharyngobranchial	absent	absent	reduced
Infraorbitals	5th with canal enclosed; 1st contacts ventral margin of lateral ethmoid	5th open; 1st 1st contacts lateral margin of lateral ethmoid	5th open; 1st contact is variable, usually ventro-posterior suface of lateral ethmoid
Cleithrum with dorsoposterior process	absent	present	present
Vertebrae	Abdominal Caudal 58–60	21–29 24–31	12–13 80+
Parapophyses	Slightly developed	Extensively developed	Variable but never as in *Merluccius*

MERLUCCIID CHARACTERS

From the foregoing comparisons it is clear that *Macruronus* differs from *Merluccius* in several features (summarised in Table I); most are autapomorphic and in this respect *Macruronus* is no less widely divergent from *Merluccius* than from any other gadoid. There are, however, seven shared characters between the two genera which at face value appear to be synapomorphic, *viz*:

1. V-shaped frontal crest; 2. fusion of supraoccipital crest with 1st neural spine; 3. palatine origin of muscle A1b; 4. prootic transverse septum; 5. absence of RLA nerve; 6. reduced first pharyngobranchial; 7. high number of abdominal vertebrae.

1. *V-shaped frontal crests*

According to Regan (1903) both *Macruronus* and *Merluccius* possess frontals bearing an anteriorly divergent ridge or crest. This V-shaped frontal crest pattern has been considered as a character for the Merlucciidae. However, the conditions in *Macruronus* and *Merluccius* are quite different. In *Macruronus* the medial frontal crest encloses a narrow, posterior central cavity. The crest also forms the medial wall of the cavity housing the frontal sensory canal which opens anteriorly through a wide aperture (Fig. 2).

In *Merluccius* the frontal ridges are widely divergent and do not enclose a narrow central cavity but a broad, open area lacking a medial longitudinal septum and transverse foramina; frontal sensory canals lack any bony covering (Fig. 5).

Markle (1989) considered a V-shaped pattern of frontal crests to be derived and one characterising the Merlucciidae. His argument for the specialized nature of this pattern is not convincing, however, since it is based on a comparison with a similar morphology in the unrelated *Opsanus*, which Gregory (1933) thought was a consequence of forces generated by *adductor mandibulae* muscles. This is a completely unfounded functional hypothesis. In fact, the pattern of frontal ridges of *Merluccius* is not unlike that of *Bathygadus* (see Howes & Crimmen, 1990); in both the crests appear to be merely the medial walls of the frontal canals left through the attrition of a roof. This is a common attribute among gadoids and macrouroids and the V-shape pattern appears to be plesiomorphic.

2. *Fusion of supraoccipital crest with the 1st neural spine.*

As observed by Fahay (1989) in macrouroids the neural spine is ligamentously attached to the supraoccipital which is also the case in the plesiomorphic gadoid family Bathygadidae. In other gadoids there is some variability; for example in the Moridae, Ranicipitidae and most Phycidae only the tip of the supraoccipital process is embraced by the lamina of the neural spine. In Lotidae, *Lota* and *Brosme* have the supraoccipital crest firmly united with the spine, whereas in *Molva* the crest is embraced by the spine, as it is in the phycid *Gaidropsarus*.

As described above, in *Macruronus* and *Merluccius* lamina of the 1st neural spine is anteriorly extended so as to embrace almost the entire posterior area of the supraoccipital crest. Fahay's (1989) reason for interpreting the similar situation in *Steindachneria* as derived is ontogenetic fusion between neural spine and supraoccipital crest. If a similar ontogenetic situation occurs in *Macruronus* and *Merluccius* this would add support to Fahay's interpretion of its derived nature.

Although referred to here as the 1st neural arch and spine, the structure of this element and its articulation with the exoccipital and basioccipital in *Macruronus* suggests that there is more than a single element involved. The pattern of occipital-vertebral contact in 'paracanthopterygians' is confusing. According to Rosen (1985) a synapomorphy for gadiforms and some ophidiforms is the anterior position of the exoccipital facets with respect to the articular surface of the basioccipital, and the corresponding forward extension of the first neural prezygapophyses. In *Macruronus* the exoccipital facets lie in the same vertical plane as the basioccipital facet and the prezygapophyses are not anteriorly extended, nor do they abut the exoccipital facets but are joined to them ligamentously (Fig. 29A). The basal anterior extension of the neural arch, likewise does not form a firm union with the sloped dorsoposterior surface of the exoccipital articular extensions, but is ligamentously attached in the same way as each vertebral neural prezygapophysis is attached to the preceding centrum. Grounds for believing that two arches are involved in the first neural element are the presence of a prominent vertical ridge down the posterior part of the neural spine and a correlated change in the direction of the bony striae from anterodorsal to posterodorsal; furthermore, two hollow shafts are present within the neural spine (Fig. 29B). I suspect that the first neural spine has become dissociated from its centrum which itself has become separately incorporated into the basioccipital (Fig. 29A). Similarly, in *Merluccius* there is no proper exoccipital facet, the terminal points of the bone being hollow and joined ligamentously to the neural arch (Figs 5A; 8). Incorporation of a first centrum within the basioccipital was suggested by Faruqui (1935) from an ontogenetic study of *Melanogrammus*.

3. *Palatine origin of muscle A1b*

Howes (1988) noted that in *Macruronus*, *Lyconus* and *Merluccius* the anterior section of *adductor mandibulae* muscle A1b originates from the lateral face of the palatine. However, in *Macruronus* and *Lyconus* the muscle originates from a deep ventral cavity confluent with a similarly deep ectopterygoid channel (p. 85). Only in *Merluccius* does the muscle originate from a lateral fossa.

Other differences between the three genera were noted by Howes (1988); pinnate nature of muscle A1a and the more anterior origin of A1b in *Macruronus* and *Lyconus*, having the correlated effect of displacing the ramus mandibularis of the trigeminal nerve past the posterior point of the muscle rather than running across it as in *Merluccius*. In all three taxa muscle A1b occupies a medial plane as A1a, as in more plesiomorphic gadoids (eg Bathygadidae, Moridae). Like those taxa, however, *levator arcus palatini* is extensive covering the upper part of *adductor mandibulae* A1. In outer aductor muscle morphology both *Macruronus* and *Lyconus* differ appreciably from *Merluccius* (Howes, 1988).

4. *Prootics with transverse septum*

In both *Macruronus* and *Merluccius* each prootic bears a medial process which sutures with its partner in the midline forming a transverse septum (p. 83).

Merluccius has a ventromedial perforation in the septum from which the recti muscles originate. In this sense the prootic cavity acts as a posterior myodome. In *Macruronus* the recti originate from the medial surfaces of the ascending processes of the parasphenoid, which is also the condition in other gadoids. Only in Gadidae is there a similar prootic extension (Fig. 6D) but in this taxon the processes remain separated from one another in the midline and form broad shelves. As in other gadoids the recti muscles originate anteriorly to the shelf, entirely within the boundary of the parasphenoid. The septal walls in *Macruronus* are medially thickened and posteriorly convex, and stem from the anterior border of the prootic. In contrast, those of *Merluccius* are of equal thickness, horizontal, posteriorly concave and extend from the prootic walls.

In Moridae there occurs a unique condition where, rather than the prootics meeting across the midline, the ascending processes of the parasphenoid are reorientated transversely and are sutured in the midline forming a septum comparable to that formed by the prootics in *Macruronus* and *Merluccius* (Fig. 6C). The recti muscles originate from the anterior facing surfaces of the parasphenoid processes.

Absence of a posterior myodome in gadiform fishes is considered derived (see Patterson, 1975), a feature most probably due to the modification of the anterior part of the prootic in forming the common optic-trigeminal foramen. In *Merluccius* development of a posterior myodome with medial extensions of the prootic forming its roof is undoubtedly a secondarily derived state. In this respect *Merluccius* differs from both *Macruronus* and Gadidae, in which taxa the recti muscles originate anteriorly to the prootic cavity. Despite this difference, prootic morphology of *Merluccius* has greater similarity to that of Gadidae than to *Macruronus*. In the two former taxa the medial extension is horizontal, emmanating from the prootic side-wall whereas in *Macruronus* it is vertical, extending from the anterior wall. The condition in *Merluccius* is considered derived from the gadid, whereas that of *Macruronus* has been independently evolved.

5. *Absence of the ramus lateralis accesorius (RLA) nerve.*

Too few taxa have been surveyed for this character to say with assurance that absence of RLA is unique to *Macruronus* and *Merluccius*. In other gadoids presence of a foramen in the cranial roof for the dorsal branch of the RLA is an indication of its dorsal ramification.

Macruronus and *Merluccius* have flat crania and both have more complex, but different, insertion of the epaxial musculature than other gadoids. *Merluccius* has an exposed posttemporal whereas in *Macruronus* it is covered by muscle fibres. Loss of RLA is possibly correlated with absence in both taxa of mucoserous pores (genipores of Svetovidov, 1948) since the dorsal branch of RLA is responsible for innervating epidermal cells. Furthermore, the lateral line in both genera is more elevated along the body than in other gadoids.

Further investigation of RLA pathways is required to determine whether these factors are correlated. On face value absence of RLA might be considered synapomorphic loss for *Macruronus* and *Merluccius*, but in the light of distribution of other, positive, synapomorphies, this negative one is regarded as homoplastic.

6. *Reduced 1st pharyngobranchial.*

Markle (1989) noted the reduction and lack of ossification of pharyngobranchial 1 in gadoids other than the Melanonidae, Moridae and Steindachneridae. Pharyngobranchial 1 is reduced and cartilaginous in Bathygadidae, considered a plesiomorphic gadiform lineage (Howes, 1988; Howes & Crimmen, 1990). Widespread reduction of this element throughout gadoids cannot therefore justify its use as a synapomorphy linking *Macruronus* and *Merluccius*.

7. *Numerous abdominal vertebrae.*

Markle (1989) considered a high number of abdominal vertebrae (20 or more) to be synapomorphic for a group of gadoids comprising the Gadidae, Lotidae and Merlucciidae. *Macruronus* has 19–21, *Merluccius* 21–29 and in this respect is the more derived taxon. In fact, *Macruronus* has fewer abdominal vertebrae than the lotids *Lota* and *Molva* (respectively with 23–26; 25–36), the gadids *Eleginus* (21–24), *Gadus* (18–22), *Merlangius* (20), *Microgadus* (17–22), *Micromesistius* (24–26), *Pollachius* (20–23) and the muraenolepid, *Muraenolepis* 20–21 (data from Fahay & Markle, 1984).

Macruronus has 58–60, caudal vertebrae which far exceeds the number in *Merluccus* (24–31), but is exceeded by the other merlucciid, *Lyconus* (72 in the only available specimen, with broken-off tail). In other 'tail-less' gadoids, bathygadids have 70+; *Steindachneria*, *ca* 80.

In view of its widespread distribution, a high number of abdominal vertebrae cannot be taken as synapomorphic for *Macruronus* and *Merluccius*. Similarly, numerous caudal vertebrae in both gadoid and macrouroid taxa suggest a plesiomorphic condition. It follows, therefore, that taxa with reduced numbers of caudal vertebrae are the more derived. It may even be that the symmetrical caudal skeleton of more derived gadoids is a feature acquired in conjunction with reduction of a tapered tail (p. 106).

In summary, none of the seven characters listed above as possible synapomorphies between *Macruronus* and *Merluccius* can, under detailed scrutiny, be upheld. Indeed, *Macruronus* also lacks those characters which I consider to delimit the subgroup of gadoids which contains *Merluccius*. These synapomorphies are:

1. Posterohyal-interopercular joint.
2. Cone-shaped lateral ethmoid
3. Hyomandibular with lateral shelf

1. *Posterohyal-interopercular joint.*

Lauder & Liem (1983: 150) pointed out that 'Gadids and merluccids (*sic*) share an epihyal-interopercular joint' which they described as a medially directed process stemming from the interopercular and articulating with the posteroventral corner of the posterohyal (epihyal). Howes (1989) and Markle (1989) have also referred to this feature as a synapomorphy uniting a subgroup of gadoids; Gadidae, Lotidae, Ranicipitidae, Muraenolepididae, Phycidae. Bregmacerotidae and Merluccidae. Both authors treated *Macruronus* as a merlucciid and as possessing this synapomorphy, but in fact, the taxon lacks this feature. Although the interopercular bears a depressed, cartilaginous articulatory surface, there is no strongly developed osseous process which forms an interopercular socket (p. 88).

2. *Cone-shaped lateral ethmoid.*

In comparing the Eocene gadoid *Rhinocephalus* to *Merluccius*, Rosen & Patterson (1969) remark on the shared character of a cone-shaped, posteriorly open, lateral ethmoid also being present in gadids.

Merluccius, displays the characteristic cone-shape only poorly since the lateral ethmoid wing is thickened, directed outward and has a broad curvature (Fig. 30A). I agree, however, that a characteristic cone-shaped morphology of the lateral ethmoid is a feature common to certain gadoids. It is present in all genera of Gadidae examined, *viz Gadus*, *Pollachius*, *Theragra*, *Merlangius*, *Melanogrammus*, *Trisopterus* (Fig. 30C). Among the Lotidae it is clearly evident in *Molva*, *Brosme* and *Lota*, despite the lateral ethmoid flaring outward. Among Phycidae, *Gaidropsarus* and *Ciliata* (Figs 30B & D), although both having a laterally directed ethmoid wing nonetheless preserve the cone-like

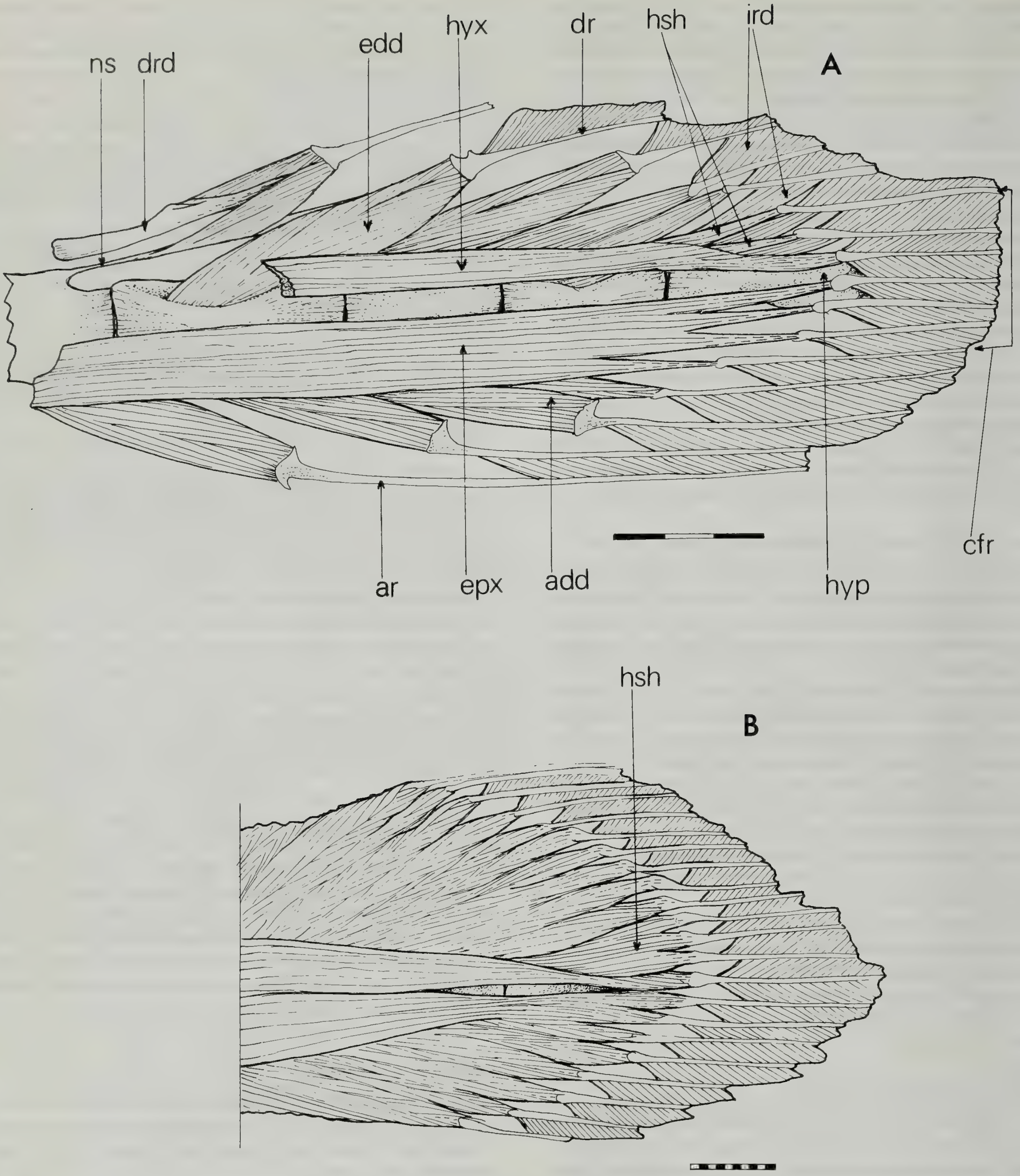

Fig. 27 Caudal fin muscles in lateral views of; A, *Macruronus magellanicus* (superficial musculature removed; BMNH 1936.8.26: 358–36) and *Merluccius capensis* (1935.5.2: 118–119).

shape, which in *Ciliata* is virtually tubular. In *Phycis*, however, the lateral ethmoid wing is a broad, downwardly curved lamina showing no trace of modification. In the Ranicipitidae, the lamina is thin and directed outwards in a near-horizontal plane (Fig. 30E), while that of Muraenolepididae is narrow, thick and downwardly directed (Howes, 1987; fig. 4b). In both latter families the lateral ethmoid appears much modified and does not exhibit any evidence of a gadid morphotype. In other gadoid families the lateral ethmoid wing has, what is considered to be the plesiomorphic form namely, a broad, downwardly directed lamina (typically in Bathygadidae, Howes & Crimmen, 1990; fig. 2B).

As far as *Macruronus* is concerned, the lateral ethmoid bears no resemblance to the gadid-type, nor to the plesiomorphic form, rather it is intermediate. Unlike *Merluccius*, however, which bears traces of a cone-shaped, gadid-type

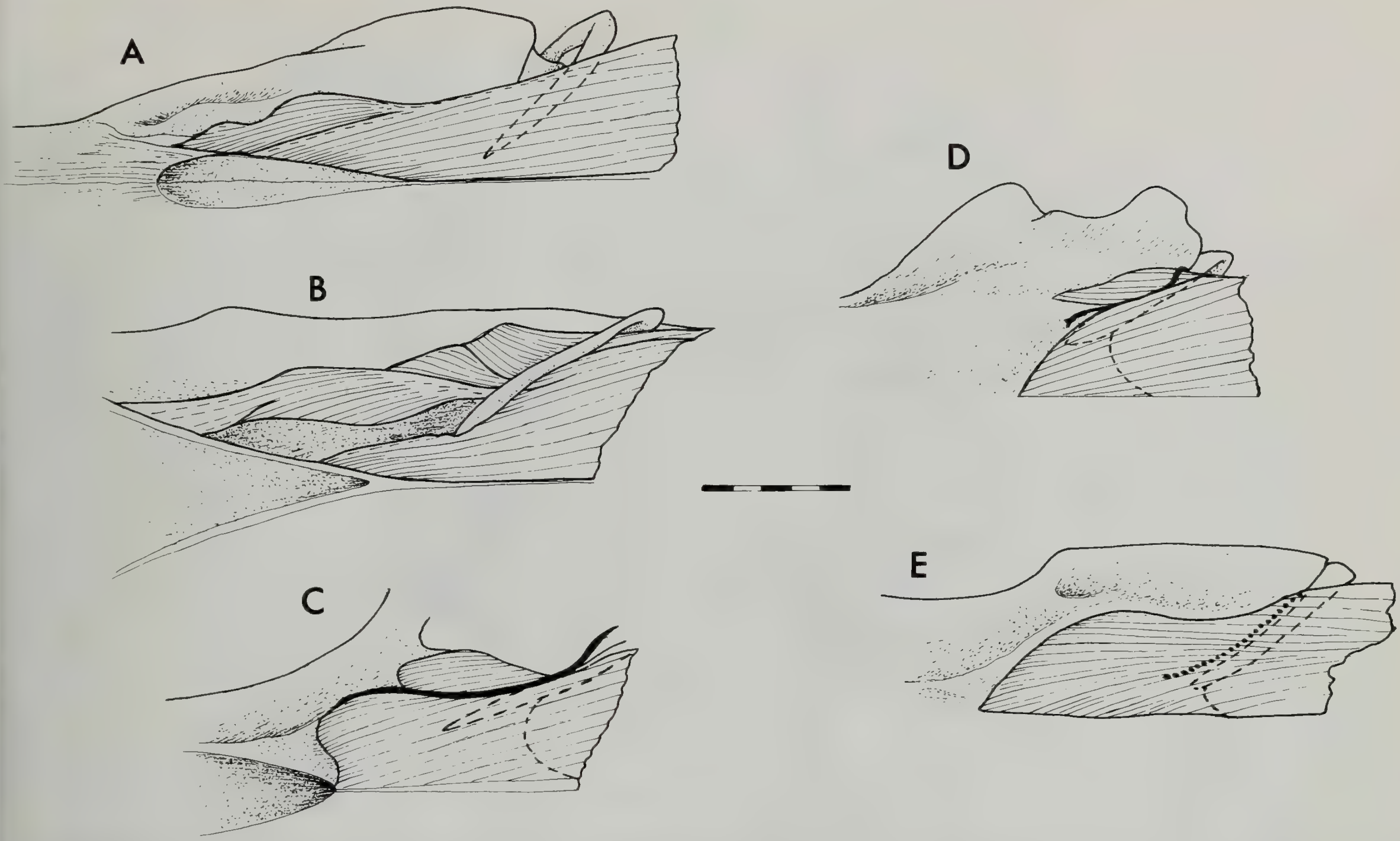

Fig. 28 Epaxial muscle insertion (dorsal aspect) of; A, *Macruronus magellanicus* (BMNH 1936.8.26: 342–351); B, *Merluccius merluccius*, (1971.7.21: 44–57); C, *Lepidion eques*, (1984.3.21: 1–25); D, *Steindachneria argentea*, (1963.2.25: 335–9); E, *Gadus macrocephalus* (1984.12.5: 30–5). Outlines of posttemporal and posterior boundary of the epioccipital are indicated by dashed lines; the RLA nerve is shown as solid black but where covered by muscles is indicated by dotted line.

morphology, *Macruronus* possesses no such feature and its lateral ethmoid appears merely to be a derived modification of the plesiomorphic, rather than of the gadid, type.

3. *Hyomandibular with lateral shelf*

A lateral flange of the hyomandibular is not an uncommon feature among teleosts and, in itself, is probably plesiomorphic. However, a group of gadoids including *Merluccius*, Gadidae, Phycidae (part) and Lotidae possess a long, broad lateral shelf from which originates the inner part of the adductor musculature. In *Merluccius* the flange slopes ventrally and is prolonged by two processes, named by Inada (1981: 78) the intermuscular and preopercular (p. 88). No other gadoid taxa possess such a hyomandibular feature and it considered synapomorphic for the four (Figs 14A & B).

DISCUSSION

Regan (1903) noted 'The extreme interest of the genus *Macruronus*... has not yet been appreciated'. That appreciation is now realised through this study in which it is demonstrated that *Macruronus* exhibits features which question earlier concepts of gadoid phylogenetic relationships.

Relationships of *Macruronus* with *Lyconus* and *Lyconodes*

Following Norman's (1966) classification, Marshall's (1966) recognition of relationship between *Macruronus*, *Lyconus*, *Lyconodes* and *Merluccius* has not been seriously challenged (although Marshall, 1973, placed *Macruronus* and *Lyconus* as family *incertae sedis*). Cohen (1984) noted that '*Macruronus* is basically a *Merluccius* with a much reduced caudal fin', and that '*Lyconus* ... is probably related to *Merluccius*'. On the contrary it seems that *Lyconus* and *Macruronus* are closely related and are phylogenetically widely separated from *Merluccius*.

Günther (1887) established the family Lyconidae to contain the genus *Lyconus* known then from a single small specimen, named as *L.pinnatus* collected in the South Atlantic. Subsequently, Holt & Byrne (1906) described a second species, *L.brachycolus* also based on a single specimen from the northeastern Atlantic. Brauer (1912) recorded three other small specimens of *L.pinnatus* from the Indian Ocean.

Lyconodes was described by Gilchrist (1922) from a single specimen and distinguished from *Lyconus* by its lack of anterior canine teeth, prolonged anterior dorsal rays and in having the gill-membranes united at the isthmus.

I have examined the type specimens of both *Lyconus* species but have not seen that of *Lyconodes*. The *Lyconus* types are both in poor condition, lacking their tail region and

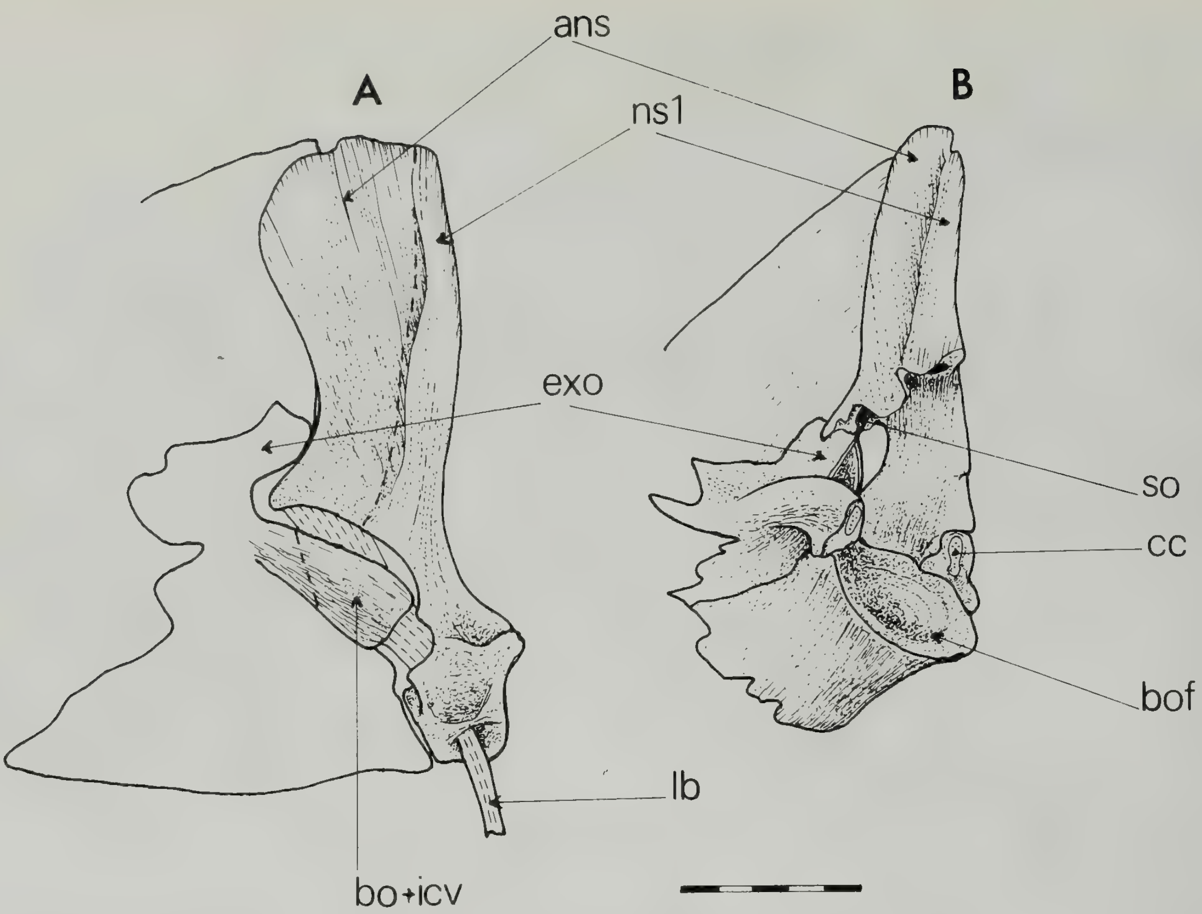

Fig. 29 *Macruronus magellanicus*, relationship of cranium and anterior vertebral elements. A, lateral view; B, ventrolateral view in which 1st centrum and lower part of left side of neural spine have been removed (BMNH 1936.8.26: 352–7, skeleton).

having damaged fins. The type of *L. pinnatus* is in very poor condition, having damaged jaws (Fig. 33). *Lyconus pinnatus* differs from *L. brachycolus* in having long, slender gill-rakers along the outer side of the first gill-arch (4 on the epibranchial + 12 on the ceratobranchial), whereas those in *L.brachycolus* are short, flat and have spinous dorsomedial surfaces. In this respect, *L.pinnatus* resembles *Macruronus*. According to Günther's (1887) description, *L.pinnatus* has a single canine-like tooth either side of the vomer (the teeth have now disappeared but their sockets remain visible); *L.brachycolus* has five and *Macruronus magellanicus* 6 or 7, and *M.novaezelandiae* 12 or more. The origin of the pelvic fins in both *L.pinnatus* and *Macruronus* lie beneath that of the pectorals, whereas in *L.brachycolus* (and *Lyconodes*) they are set forward.

Radiographs of both *Lyconus* species indicate a similar cranial morphology to that of *Macruronus*. In *L.pinnatus* the dorsal fin rays are broken off at their bases and externally it is impossible to distinguish two separate dorsal fins. The radiographs show, however, that there is a distinct gap between the 10th and 11th radial, which corresponds to the interdorsal space of *Macruronus*. For *L.brachycolus* a radiograph does not reveal such a gap, indeed, the 9th and 10th dorsal radials are closer together than are the others, but Holt & Byrne (1906) noted an inflection of the dorsal fin outline at the 10th dorsal ray.

Although *Lyconus* is said to have the gill membranes free from the isthmus, it appears that in *L.brachycolus* there is such a connection judging from the remains of membrane attaching to the isthmus, but that it has been torn away. Thus, although *Lyconus pinnatus* differs from *Lyconodes* in this respect, *L.brachycolus* does not and it fails as a feature distinguishing the two genera.

Lyconus brachycolus (Fig. 34) possesses apomorphies shared with *Macruronus*, namely an elongate anterior extension of the retroarticular, an enclosed sensory canal on the 5th infraorbital and a deep autosphenotic notch which accommodates the dermosphenotic (Fig. 33). I have been unable to determine whether *L.pinnatus* possesses the elongate retroarticular, but it certainly has a similar infraorbital and sphenotic morphology to *Macruronus*. *Lyconus pinnatus* differs from *Macruronus* only in the lower number of jaw teeth and seems to represent a juvenile specimen of that genus but on the available evidence is impossible to say to which species of *Macruronus* it belongs (p. 108).

Lyconus brachycolus differs from *Macruronus* in having a single dorsal fin and a more anterior position of the pelvic fin origin, features in which it appears to be the more derived taxon. In view of the apomorphies shared only with *Macruronus* it must be regarded as the sister taxon of that genus.

The phylogenetic position of *Lyconodes* cannot at present be determined. It too shows juvenile features in its extended pectoral fin rays (the type is only 45mm TL). Marshall (1966) has pointed out the posterior position of its pelvic fin in relation to the pectoral fin origin, and if it were not for this feature I would regard it as a juvenile of *Lyconus brachycolus*.

Recognition of *Lyconus* as a synonym of *Macruronus*, of *Lyconus brachycolus* as a distinct taxon, and the lack of close phylogenetic affinity of these taxa with *Merluccius* requires:

1. establishment of a new genus group name for *Lyconus brachycolus*. 2. recognition of a separate family to contain that taxon and its sister group, *Macruronus*.

In order to recognise *Lyconus brachycolus* as a distinct taxon

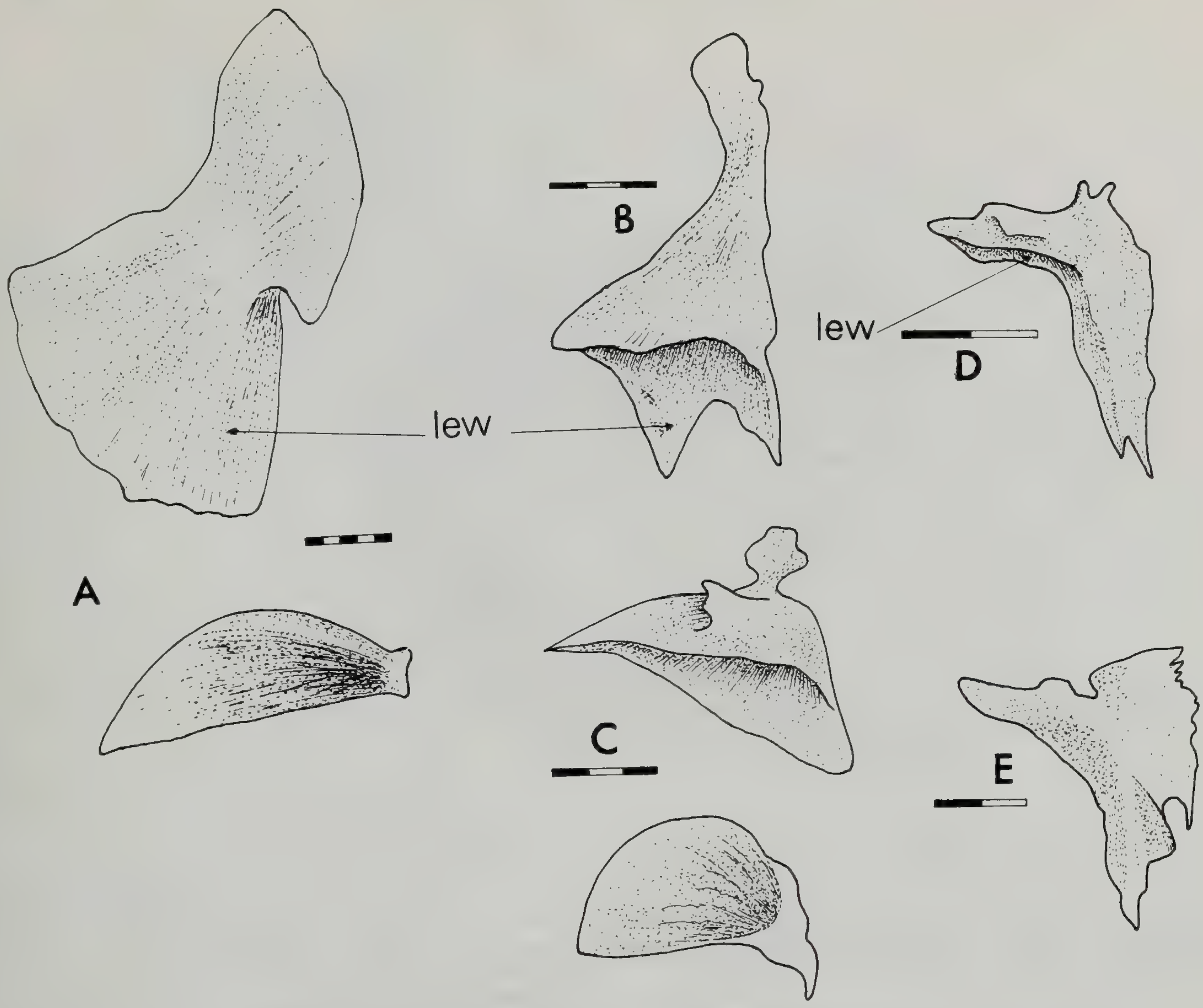

Fig. 30 Lateral ethmoids of; A, *Merluccius merluccius* in ventral and posterior views: B, *Gaidropsarus vulgaris*, ventral view; C, *Trisopterus luscus*, in ventral and posterior views; D, *Ciliata mustela* and E, *Raniceps raninus*, both ventral views (all unregistered skeletal specimens from the Ford Collection).

and sister group to *Macruronus* one may either expand the latter genus in order to contain it simply as another species, or emphasise its anatomical distinctiveness by recognising it as a subgenus or genus. This decision is a matter of opinion since at present there is no rigorous cladistic analysis of all gadoid families, i.e. no nested subsets by which one may judge the 'taxonomic-level' of a particular lineage. Rather than proliferate an already unstable classificatory system with more higher-level categories I have opted to recognise *Lyconus brachycolus* as representing a subgenus of *Macruronus*, referred to as *CYNOGADUS*, both for its characteristic canine teeth and for its overall resemblance to its macrouroid 'counterpart' *Cynomacrurus* (see Appendix, p. 108).

Recognition of a separate family to contain *Macruronus* is taxonomically justifiable and necessary in order to indicate the relationships of *Macruronus* to other gadoids. Norman (1966) had already provided a family name, then recognised as a subfamily of the Merlucciidae, and here referred to as the MACRURONIDAE.

The relationships of the Macruronidae to other gadoids form the remainder of this discussion.

Relationships of the Macruronidae with other gadoid families

Knowledge of gadoid interrelationships is poor, indeed, even the recognition of higher taxa as subfamilies or families is based on the opinion of each author rather than a consensus arrived at by employing rigorous methods of comparative analysis (see for example, Markle, 1982; Cohen, 1984).

Howes (1989) attempted to recognise lineages, ranked as families and recognised primarily on the basis of myological characters. Markle (1989) too has attempted a cladistic analysis based on a wider range of anatomical, but mostly osteological, characters. Both Markle's and my cladograms include unresolved polychotomies and suffer through lack of anatomical data and knowledge of character polarity. That said, our views of family relationships are not so radically different. For example, we both regarded the Moridae and Steindachneriidae as being closely related, the Muraenolepididae and Phycidae as being part of the same major group, and the Gadidae and Lotidae as belonging to a more derived lineage. We differed, however, in our view of the relationship of the Merluccidae. Markle recognised it as the sister-group to the Gadidae and Lotidae while I placed it as the sister taxon to a group comprising five families within a broader complex termed 'higher gadoids'. (This category was recognised on the basis of a medial shift of the entire *adductor mandibulae* muscle A1b and loss of a palatine-lateral ethmoid ligament.) Nonetheless, both Markle and I, in common with other authors, recognised the Merlucciidae as a monophyletic lineage. My dispute with that supposition now leads me to reevaluate the phylogenetic positions of the Merlucciidae (now including the single extant genus *Merluccius*) and establish that of the Macruronidae.

Merluccius clearly belongs to the complex of 'higher

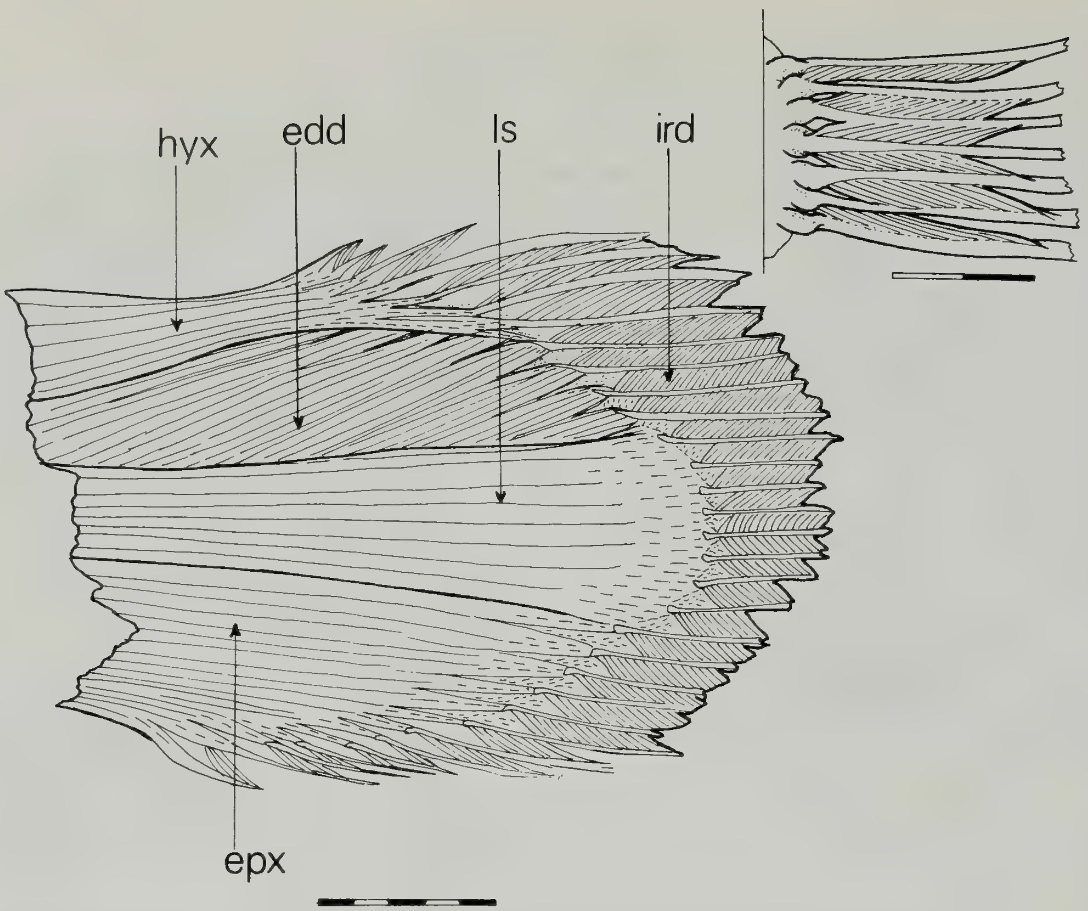

Fig. 31 Caudal fin musculature of *Urophycis regia* (BMNH 1985. 6.6: 109–119) showing superficial layers. Above, right, *interradialis* connection between medial caudal fin rays of *Gadus macrocephalus* (BMNH 1984.12.5: 30–33).

gadoids' in possessing a derived arrangement of the *adductor mandibulae* musculature (Howes, 1988), a well-developed articulatory facet on the interoperculum for the interhyal (p. 99) and a firm articulation between the dorsal process of the first infraorbital and the posterior face of the lateral ethmoid (p. 84). *Merluccius* also shares with the Gadidae, Lotidae and some Phycidae a strong lateral flange of the hyomandibular from which originates part of the *adductor mandibulae* musculature (p. 101), and shares a cone-shaped lateral ethmoid wing with the Lotidae and Phycidae. *Merluccius* also shares with phycids, gadids and lotids the tendency of attrition of the anterior wall of the prootic so that the trigeminal foramen is eroded into a notch. Only with the Gadidae does *Merluccius* share a medial prootic shelf (p. 98).

The Macruronidae lacks all of these 'higher gadoid' features and although specialized in many respects, has a generally low-level gadoid morphotype. In its caudal fin skeleton, the Macruronidae is hardly different from the Euclichthyidae, except that X and Y bones are lacking. Their absence is one the Macruronidae shares with the Melanonidae, Gadidae and Lotidae. Since the absence of 'higher gadoid' synapomorphies exclude a close relationship between the two latter families, the loss would appear to be an independent one. Likewise, there are no other identified synapomorphies that suggest a close relationship between the Melanonidae and Macruronidae.

The melanonid caudal skeleton is shown by Paulin (1983: fig. 5a) to possess, what I interpret (the figure is not labelled) as an autogenous parhypural; fused first and second hypurals; a compound centrum bearing lower hypurals separated from the upper, and two epurals. The separation of the upper hypurals (which I have not been able to confirm in the specimen to hand) suggests a more primitive organization of the caudal skeleton than in *Macruronus*, and one not far removed from the Moridae in which all the upper hypurals are separated distally. I have not found in the Melanonidae, the connection of *interradialis* muscles between the caudal fin and dorsal and anal fins.

The Macruronidae shares no detectable synapomorphies with the Steindachneriidae, whose phylogenetic position is ambiguous. The Steindachneriidae lacks a caudal fin skeleton; has a primitive connection of the palatine with the lateral ethmoid wing and a primitive jaw muscle morphotype (Howes, 1987; 1988).

Contact of the palatine with the mesethmoidal portion of the lateral ethmoid (Howes, 1987) and complexity of jaw aductor musculature places the Macruronidae amongst the majority of gadoid families and its possession of a caudal skeleton having complete fusion of the upper hypurals into a single plate places it at a higher level of morphological specialization than Moridae and Euclichthyidae.

Euclichthyidae and Bregmacerotidae were considered by Howes (1988) as members of the 'higher gadoids'. However, re-examination of these taxa shows that an interopercular-interhyal joint is absent in *Bregmaceros* and only a shallow interopercular fossa is present in *Euclichthys*. *Bregmaceros* has, according to Markle (1982) attained the greatest internal and external caudal symmetry among gadoids. The relationships of the Bregmacerotidae are unclear and are positioned on the accompanying cladogram (Fig. 35) on the strength of a single character, namely, absence of a palatine-lateral ethmoid ligament, but this has been found subsequently in some 'higher gadoid' species.

As expressed here (and indicated by Rosen & Patterson,

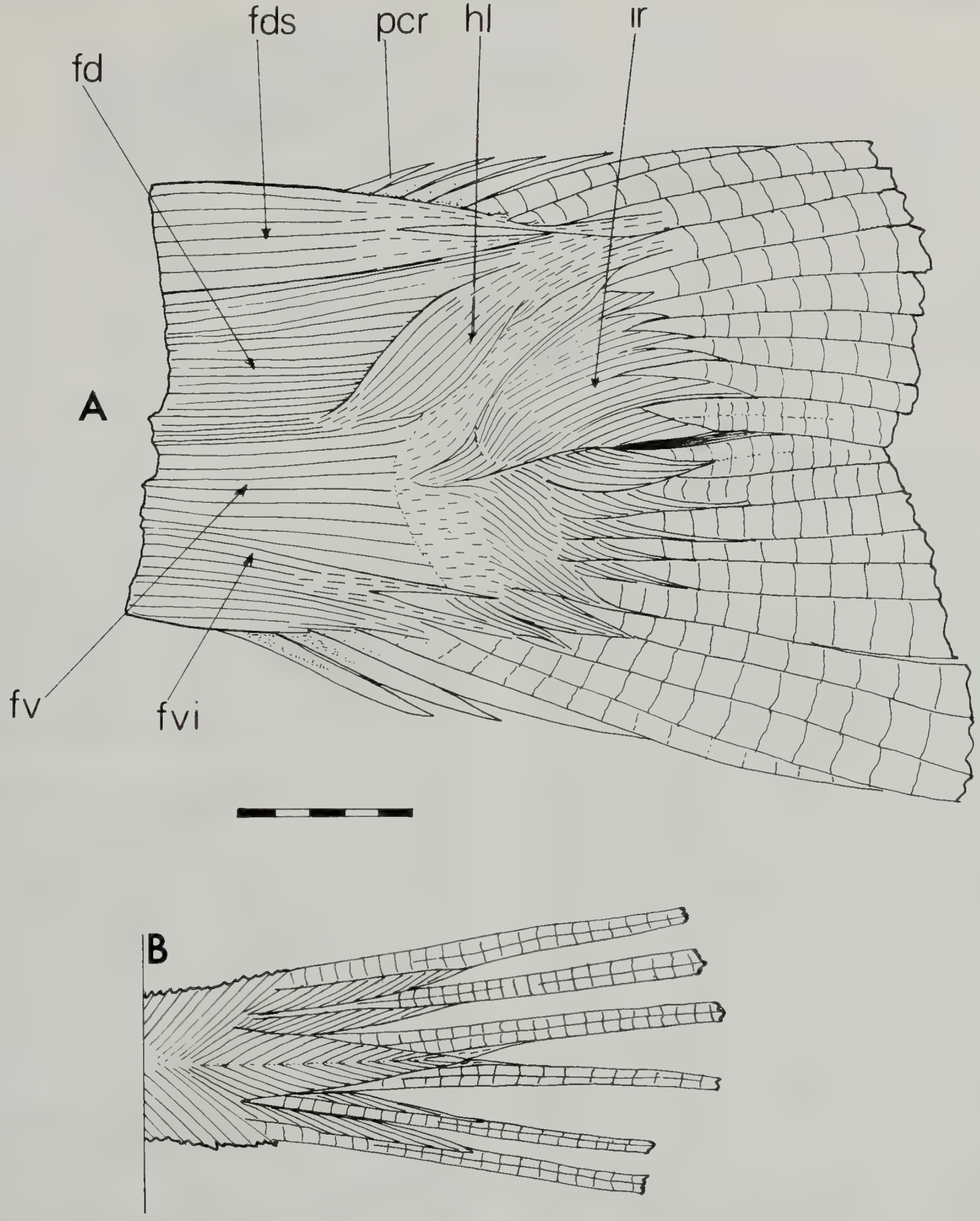

Fig. 32 Caudal fin musculature of; A, *Polymixia lowei* (BMNH 1987.12.7: 1–5); B, *Percichthys trucha* (BMNH 1935.4.23: 21–33), showing *interradialis* connections between medial caudal fin rays.

1969) the relationships of the gadoid families demonstrate a trend toward caudal fin element reduction by fusion that has been accompanied by re-organization and reduction of caudal fin musculature.

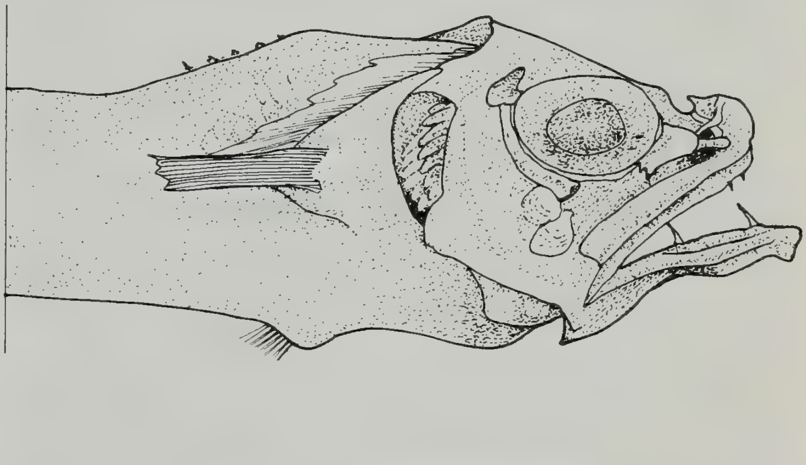

Fig. 33 *Macruronus* (*Macruronus*) *pinnatus*. Holotype, (BMNH 1876.3.4: 74). Lateral view of head and anterior body region. NB. Jaws and infraorbitals damaged and anterodorsal part of body torn.

In gadoids the muscles serving the caudal fin are 'reduced' and simplified compared with those in most other teleosts. Symmons (1979) pointed out that in *Gadus* hypochordal muscles are lacking and that there are no intrinsic muscles associated with the vertebrae and caudal fin rays other than what she termed a pair of deep dorsal and ventral flexores (which I have referred to as a hypural segment of hypaxial muscle, there being only a dorsal and no ventral component; p. 94). Neither is there a superficial part of the *interradialis*, a feature common in other teleosts where a sheet of superficial fibres crosses the bases or necks of the caudal rays and so interconnects widely spaced rays. Among some acanthopterygians the *interradialis* is often thickened and complex and deeply divided between the upper and lower caudal lobes (see below). In gadoids the *interradiales* connect only one ray with another and the demarcation between upper and lower regions of the fin is marked by a change of direction of muscle fibres (see above and Fig. 27). Furthermore, *interradialis* muscles occur between the so-called procurrent caudal rays. They are absent between those rays in other teleosts.

The longitudinal dorsal and ventral muscles attaching to the upper and lower caudal rays represent what I believe to be merely epaxial and hypaxial muscle bands and are thus not

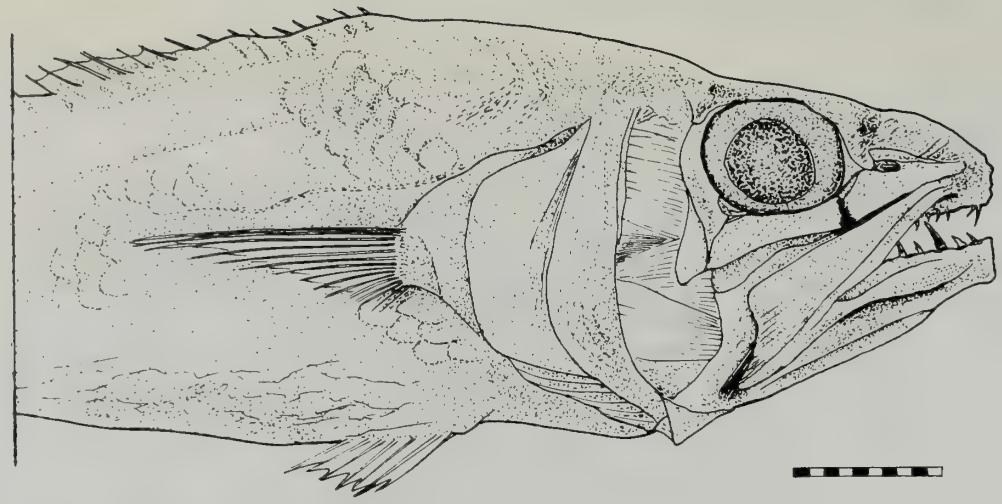

Fig. 34 *Macruronus* (*Cynogadus*) *brachycolus*. Holotype, (BMNH 1907.6.20: 15). Lateral view of head and anterior body region. NB. Infraorbitals damaged and head partially dissected.

homologous with the *flexores dorsales* and *ventrales* of other teleosts (Fig. 32). Likewise, the posterior segment running from the terminal centrum (hypural plate) and inserting on the upper caudal ray bases does not appear to be the homologue of the *hypochordal longitudinalis* of other teleosts. That muscle, in acanthopterygians at least, is separated from the *interradialis* by a hypural marginal area of thick collagenous tissue covering the bases of the caudal rays. The *hypochordal longitudinalis* in other teleosts has a long base which usually originates from a hypurapophysis, and narrows at its points of insertion. The analogous muscle segment in gadoids has a short area of origin on the anterodorsal area of the terminal centrum and broadens over its area of insertion (see Fig. 27A). Macrouroids (including *Trachyrincus*) possess a body muscle morphology similar to that of gadoids except that there is no separately identifiable posterior segment attaching to the hypural plate; the upper and lower longitudinal muscle bands connect with caudal rays.

Differences between the arrangement of the caudal fin musculature in gadoids and other investigated teleosts signify a lack of homology between the elements. The absence of complex *interradiales*, the development of those muscles between 'procurrent' caudal rays, the absence of *flexores dorsales* and *ventrales*, and *hypochordal longitudinalis* all point to the modification of the caudal fin skeleton. I would suggest that '*interradiales*' muscles of gadoids are modified *depressores dorsales* and *ventrales* since they comprise two components and occur between the 'procurrent' rays.

The taxonomic significance of caudal fin musculature has so far been overlooked. For example, in acanthopterygians there are marked differences in how upper and lower caudal fin lobes are served by *interradiales* muscles. In *Polymixia*, which represents the majority of taxa reported upon (Winterbottom, 1974; Videler, 1975), division is complete, each lobe being controlled by different bundles of *interradiales* Fig. 32A). In *Percichthys*, however, the medial rays of upper and lower lobes are connected by a single, pinnate muscle whose oppositely directed fibres are joined in a midline raphe (Fig. 32B). These and other features require a full investigation from taxonomic, phylogenetic and functional standpoints.

Complete loss of a caudal skeleton is characteristic of two gadoid families, Bathygadidae and Steindachneriidae, as well as of the Macrouroidei. In Trachyrincidae, the caudal skeleton is modified by apparent loss of various elements and a 'gadoid symmetry' is ambiguous (Howes, 1989). In its rat-tailed appearance, reduced upper hypural plate and loss of X and Y bones it is tempting to regard the Macruronidae as representing an evolutionary condition tending toward total caudal loss. Boulenger (1902) and Regan (1903) considered the gadoid caudal skeleton to be a *de novo* development from a tailless state.

If Fahay's (1989) hypothesis that Steindachneriidae is the plesiomorphic sister group of Macrouroidei, and Howes & Crimmen's (1990) suggestion that Bathygadidae is the plesiomorphic lineage of other gadiforms be accepted, then serious consideration must be given to Boulenger's and Regan's suggestions. There is, however, no comparative anatomical or ontogenetic evidence that would suggest *de novo* development and it is assumed that caudal skeleton loss has been independently derived in those various lineages (Howes & Crimmen, 1990).

To summarise; the Macruronidae forms the sister-group to a lineage comprising Bregmacerotidae, Muraenolepididae, Ranicipitidae, Phycidae, Lotidae, Gadidae and Merlucciidae (Fig. 35). Relationships of these families to one another remain to be more completely resolved as do those of the 'lower' gadoids, Melanonidae, Steindachneriidae and Bathygadidae.

Concerning the Eocene merlucciid *Rhinocephalus*, this fish appears correctly assigned to this family. The pattern of frontal crests, infraorbital morphology and arrangement of otic bones, including an aperture bounded by the prootic and pterosphenoid for the trigeminal nerve tract, all indicate its merlucciid affinity. Although the caudal skeleton of *Rhinocephalus* is unknown, those of other Eocene gadoids resemble morids (Rosen & Patterson, 1969: 432–3). If *Rhinocephalus* proves to have an advanced gadoid caudal skeleton (as in *Merluccius*) then it would suggest that the division between 'lower' and 'higher' gadoids would have been established by the Eocene.

ADDENDUM

After this paper had been accepted for publication, two papers appeared which contain phylogenetic relationship hypotheses of *Macruronus*. Both Okamura (1989) and Inada (1989) treat *Macruronus* and *Lyconus* as a sister group to

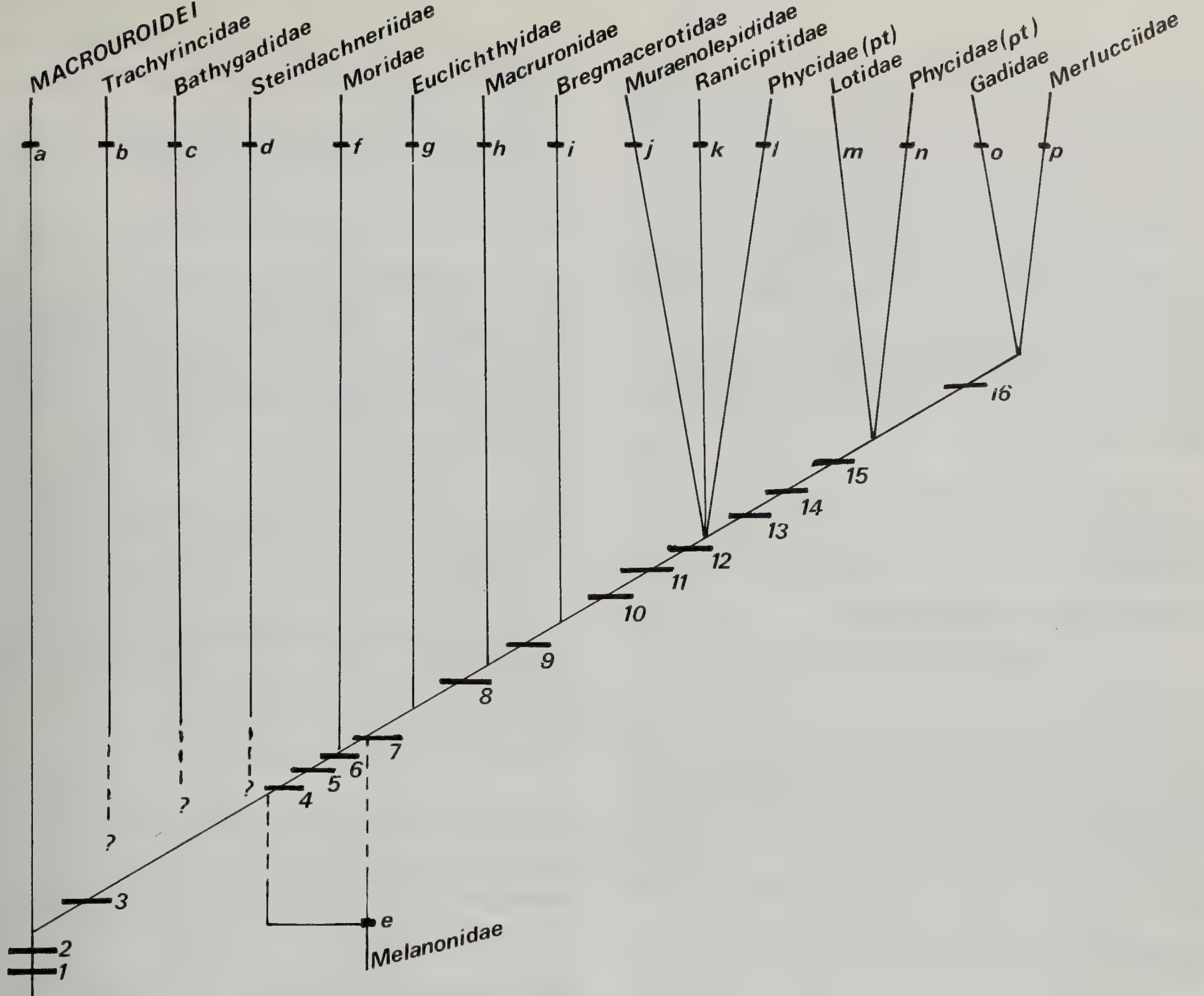

Fig. 35 Cladogram of gadoid relationships. Synapomorphies relating families: **1**, *Levator arcus palatini* muscle lies lateral to *adductor mandibulae*; **2**, Absence of pars jugularis (a single opening serves for the transmission of all cranial nerves and vessels. **3**, *Rectus communis* muscles attached to *sternohyoideus*; **4**. X and Y bones in caudal skeleton (lost in Melanonidae, Macruronidae, Lotidae and Gadidae; presumably also in Trachyrincidae, Bathygadidae and Steindachneriidae; **5**, Caudal fin muscles modified, *interradiales* connect caudal fin rays with dorsal and anal rays; **6**, Palatine contacts the mesethmoidal part of lateral ethmoid; **7**, Medial shift of muscle A1b; **8**, Complete fusion of upper hypurals into single plate. (According to Markle (in litt.) upper hypural plate of *Raniceps* is bifurcate and ontogenetically displays more than two upper hypurals). This demonstration of ontogenetic fusion could thus be considered a character reversal; distribution of other synapomorphies do not support the view that *Raniceps* occurs at a lower phylogenetic level; **9**, Loss of lateral ethmoid-palatine ligaments; **10**, 1st infraorbital contacts posterior face of lateral ethmoid wing; **11**, Posterohyal articulates with an interopercular fossa whose rim forms a 'stop' to its posterior movement; **12**, *Rectus dorsalis* muscle inserts on pharyngobranchial 4 in addition to 3 (exceptions: *Merluccius*, inserts only on 3; *Muraenolepis*, inserts only on 4); **13**, Hyomandibular with lateral shelf; **14**, Cone-shaped lateral ethmoid wing; **15**, Attrition of the prootic anterior border with often, in conjunction with pterosphenoid; formation of separate foramen for trigeminal and hyomandibularis nerves; **16**, Medial prootic shelf.

Synapomorphies for lineages: **a**, Macrouroidei; loss of interopercular- subopercular ligament; many other synapomorphies, discussed in Howes & Crimmen, 1990; **b**, Trachyrincidae; *Adductor mandibulae* A1 muscle a single element, nasal bones extended, palatine immobile (Howes, 1987, 1988; 1989), caudal fin skeleton 'rudimentary' (Howes, 1988b and this text); **c**, Bathygadidae; pectoral branch of RLA nerve hypertrophied (Howes & Crimmen, 1990); **d**, Steindachneriidae; luminescent organs, wide separation between anus and urogenital opening, enlarged anal radial and compound first anal fin ray (Fahay, 1989); **e**, Melanonidae; specialized neuromast pattern, ectopterygoid teeth, loss of *intermandibularis* muscle; **f**, Moridae; primitive otophysic connection (Paulin, 1983), swimbladder with horizontal septum (Paulin, 1988), parasphenoid with transversely aligned ascending process (this text); **g**, Euclichthyidae; jugular placed and reduced pelvic girdle, pelvic rays and anterior rays of anal fin extended, lateral ethmoid wing transversely convex; **h**, Macruronidae; retroarticular with anteroventral prolongation, prootics form a wall across the midline, modified caudal fin skeleton, modified infraorbital bones, *adductor arcus palatini* muscles originates partly from a ventral palatine fossa (this text); **i**, Bregmacerotidae; single first dorsal fin ray articulating with an angled radial lying along the supraoccipital crest, advanced symmetry of the caudal fin (Markle, 1982) reduced metapterygoid and operculum (pers. obs.) *adductor mandibulae* muscle reduced to a single element (Howes, 1988); **j**, Muraenolepididae; derived palatine morphology (Howes, 1987), *rectus dorsalis* muscle inserts only on pharyngobranchial 4 (Howes, 1988); **k**, Ranicipitidae; first dorsal fin with 3 rays, lateral line reduced; **1**, Phycidae (*Phycis*, *Urophycis*) *epaxialis* muscle inserts on operculum (also shared with the *Muraenolepis* and *Lota*), frontals fused (shared with Gadidae), anterior diverticulum of swimbladder adnate to exoccipital (pers. obs.); **m**, Lotidae, no well corroborated synapomorphies for *Molva*, *Lota* and *Brosme*, those given by Markle, 1982 are, absence of pterotic spine, initial pelvic fin ray formation prior to flexion, and delayed acquisition of adult complement; **n**, Phycidae (*Gaidropsarus*, *Motella*, *Ciliata*, *Rhinonemus*), first dorsal fin comprised of several filamentous rays contained in a dorsal groove, and supported by modified radials (Markle, 1982); **o**, Gadidae; three dorsal fins, reduced and enclosed 'mucous' cavity of the frontals, frontals fused in most taxa, swimbladder with elaborate anterior diverticulae; **p**, Merlucciidae; enlarged vertebral parapophyses, hyomandibular with two long, lateral ventrally directed processes, *levator arcus palatini* muscle originates from a lateral palatine fossa, medial prootic shelves form pseudo-posterior myodome (this text)

From this cladogram, it follows that the Gadoidei are embraced by character **3**. Since, however, this feature is also encountered in some macrouroids (Howes, 1988a) its status as a synapomorphy is weakened. Alternatively, recognition of the Gadoidei by characters **5** and **6** places the Trachyrincidae, Bathygadidae, Steindachneriidae and Melanonidae as *incertae sedis*. This cladogram has since been superseded by another (Howes, 1990) in which the Muraenolepididae is aligned with the Lofidae and the second part of the Phycidae.

Merluccius. In other words, they accept the near-traditional view of the Merlucciidae (recognised as a family by Okamura and a subfamily by Inada. Both authors use characters which are regarded therein either as plesiomorphic or homoplastic. Inada's sole 'synapomorphy' for allying the three genera is the V-shaped frontal ridge, a feature discussed here and deemed plesiomorphic for gadoids. Okamura presents no evidence for grouping the three genera other than 'All characters are opposite, that is, primitive states of those of *Steindachneria*'.

I do not believe that either author has addressed the problem of merlucciid monophyly and none of the characters they present are new or are polarized through adequate outgroup analysis.

APPENDIX

Taxonomy of the Macruronidae

Family MACRURONIDAE

Macruroninae Norman 1966:196

Distinguished from other gadoid families in arrangement of dentition, having large, compressed caniniform teeth in outer row of both jaws and an inner row of small, horizontally aligned and medially directed teeth; anteriorly extended anteroventral margin of retroarticular; densely ossified 5th infraorbital and reduced 6th contained in a sphenotic-frontal notch.

TWO GENERA: *Macruronus* Günther, 1873; *Lyconodes* Gilchrist, 1922.

Macruronus

Günther, 1873: 103; type species *Coryphaenoides novaezelandiae* Hector 1889: 196
Lyconus Günther, 1887: 158; type species *Lyconus pinnatus* Günther, 1887: 158.

Subgenera: *Macruronus*; *Cynogadus* (p. 103).

Species:

Macruronus (*Macruronus*) *novaezelandiae* (Hector, 1889)

Coryphaenoides novae-zelandiae Hector, 1889: 157
Macruronus novae-zelandiae Günther, 1873: 103; 1887: 157

For description, see Waite, 1911: 180, and for bioeconomic data, Kuo & Tanaka, 1984*a*,*b*,*c*. and Patchell, 1982; for larval development, Patchell *et al.*, 1987; Bruce, 1988.

DISTRIBUTION: New Zealand, Tasmania.

Macruronous (*Macruronus*) *magellanicus* Lönnberg, 1907

Macruronus magellanicus Lönnberg, 1907: 15
Macruronus novae-zelandiae (*non* Hector) Günther, 1880: 22
Macruronus argentinae Lahille, 1915: 22

For description, see Norman (1937:49) and Inada (1986), and for bioeconomic data, Hart (1946) and Torno & Tomo (1980).

DISTRIBUTION: coastal areas and banks off southern South America.

Macruronus (*Macruronus*) *capensis* Davies, 1950

Macruronus capensis Davies, 1950: 512
Described from a single specimen, Davies distinguished this from other species on the presence of a small 'spine' and 13 soft rays in the first dorsal fin. However, there is a reduced first ray present in all *Macruronus* species and there are 13 longer rays in *M.magellanicus*. Davies also noted a supposed difference in dentition, mistakenly believing that teeth were absent in the upper jaw of *M.magellanicus* and that two rows of upper jaw teeth were a feature unique to *M.novaezelandiae*. The inner row is, however, present in *M.magellanicus* and is visible only when tissue covering the inner surface of the jaw is removed (see Fig. 11C), and so it seems likely that Davies overlooked these teeth.

Davies also maintained that the locality (off the Cape) and depth of capture (280 fms) further signified 'specific distinctiveness'. Since Davies's description further specimens have been reported (Cohen, 1986: 325).

DISTRIBUTION: Off South African Cape.

Macruronus *(Macruronus) caninus Maul, 1951*

Macruronus caninus Maul, 1951: 45

Known from three specimens; provenance uncertain, but most likely the southern coast of Madeira.

Macruronus *(Macruronus) maderensis Maul, 1951*

Macruronus maderensis Maul, 1951: 49

Known from eight specimens, all juveniles (the largest 85mm TL), taken from the stomach of an *Alepisaurus ferox*; off Madeira.

Macruronus *(Macruronus) pinnatus*

Lyconus pinnatus Günther, 1887: 158.

The type (Fig. 33) and other known specimens are all juveniles. Recorded from the south Atlantic and Indian Oceans.

Macruronus *(Cynogadus) brachycolus*

Lyconus brachycolus Holt & Byrne, 1906: 424

Known only from a single specimen from the Irish continental shelf (Fig. 34).

The species of *Macruronus* are poorly known and the distinctions between them are slight. *Macruronus* (*M.*) *magellanicus* is distinguished from *M.novaezelandiae* on the basis of its smaller eye and longer premaxillary; the two species from Madeira supposedly have fewer rays in the first dorsal fin, both are described from juvenile specimens which may be conspecific with the southern Atlantic species. Only the collection and study of more material will determine whether the described taxa represent distinct species or populational variants of a single cosmopolitan one.

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The pharyngobranchial organ of mugilid fishes; its structure, variability, ontogeny, possible function and taxonomic utility.

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Synopsis. Although a pharyngobranchial organ (PBO) has long been recognised as a characteristic feature of the Mugilidae (grey mullets), little attention has been given to its structure and function. The organ involves extreme modification of the pharyngobranchial bones of the upper gill-arch, their associated musculature and dentition. The skeletal and soft anatomical structures of the adult organ and its development are described. An hypothesis of its function as a filtering and sampling device is put forward. The taxonomic variability of the PBO among mugilid genera is catalogued and its taxonomic and phylogenetic usefulness discussed. An hypothesis of generic-group interrelationships is given based on ontogenetic and sequentially derived features of the PBO.

INTRODUCTION

The Mugilidae, commonly known as grey mullets, includes some 12 genera and *ca.* 80 species which inhabit marine inshore, estuarine, and freshwater environments in tropical, subtropical, and temperate regions of all continents. Mugilids have characteristic oral and branchial filter-feeding mechanisms. Feeding occurs in three ways: the fish forage on the benthos, in a head-down position with the mouth protruded, sucking up the surface layer of deposits which are filtered in the pharyngobranchial cavity; they stir up benthic deposits with their fins, then back into the cloud of suspended particles which are sucked in and filtered; or they selectively browse on aufwuchs (the substrate mat of algal and associated microbenthic material; see Reid (1985: p. 9) for further description) which covers submerged rock, plant leaf and root surfaces (Günther, 1861; Jordan, 1905; Hiatt, 1944; Ebeling, 1957; Odum, 1968; Hickling, 1970; Fagade & Olaniyan, 1973; Chan & Chua, 1979; King, 1988). A term sometimes applied to mullet feeding is *ilyophagous*, referring to the top-most layer of sediment (Ching, 1977).

Filtration of the selected material is presumably achieved by the gill-rakers in conjunction with a pharyngeal apparatus, referred to here as the *pharyngobranchial organ* (PBO). Given that a filter-feeding mechanism is a principle character of mugilids it is remarkable that so little attention has been given to this organ either anatomically or as a taxonomic character. It is the aim of this paper to redress that situation.

Since Günther (1861) first described the gill-arch feeding mechanism, only Drake *et al.* (1984) and, particularly, Capanna *et al.* (1974) have provided a more complete anatomical and functional description of the system. These authors pointed out that mugilid pharyngeal structures were insufficiently analysed. In our view the PBO holds promise of a character-complex valuable in diagnosing taxonomic groups. Specific and generic level differences appear to be indicated in the gross morphology of various parts of the organ (see below).

Schultz (1946) is the most recent author on generic-level mugilid taxonomy and we have relied on his revision as a basis in making comparisons of various taxa. We have also used an unpublished, but relatively widely circulated, manuscript revision by Ingham (completed *ca.* 1952). Ingham attempted a species as well as generic level revision but she, like Schultz, used only a combination of externally visible characters, *eg*., morphology of teeth and jaw bones, position of nostrils, development of adipose eye-fold tissue, scale type and morphometrics to distinguish taxa. Schultz (1946) recognised 13 genera, 3 described as new, whereas Ingham recognised 11. Trewavas & Ingham (1972) and Trewavas (1973) utilised some of Ingham's unpublished data in their respective reviews.

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Few osteological and ontogenetic studies have been made on mugilids. One of us (IJH) is engaged upon a study of mugilid ontogeny and we are confident that there are many, as yet untapped, osteological and other features which will be valuable in discovering and elucidating the interrelationships of mugilid groups.

METHODS AND MATERIALS

Gross morphology of the PBO was studied by removing the opercular bones and cutting away the gill-arches (ceratobranchials) to expose the lateral face of the organ. In specimens of *ca*. 30mm, the organ was stained with haematoxylin which enhances surface features. Internal anatomy was studied by cutting transverse and horizontal sections through the head and by removing the gill-arch *in toto*. Osteological features were examined by using cleared and alcian/alizarin stained specimens. Specimens used are in the collections of the Natural History Museum, London (BMNH) and the Dipartimento di Biologia e Fisiologia Generali, Universita' di Parma (PA). The catalogue numbers of the BMNH specimens examined in this study are given in the Figure legends, and these numbers may be used to retrieve further data concerning localities of capture etc. The PA specimens were all collected from the Mediterranean (mouth of the River Magra, Italy) between 1984 and 1986.

Abbreviations used in text and figures

afb, anterior fat body; av, anterior valve; bc, buccal cavity; bl, Baudelot's ligament; br, brain; cbp, ceratobranchial process; dt, distal teeth; eb1–4, epibranchials (1 to 4); ec, epithelial cushion of PBO; em, ethmoid fat body; epx, epaxial musculature; da, denticulate area; do, dorsal aperture of sulcus; ga1–5, gill-arches (1 to 5); gf, gill filaments; gt, gut; ht, heart; iac, interarcual cartilage; li2, li4, 2nd and 4th *levator internus* muscles; ms, medial septum of PBO; nc, neurocranium; ns3, 3rd neural spine; os, oesophagus; pb1–4, pharyngobranchials (1 to 4); pbk, 3rd pharyngobranchial keel; pbo, pharyngobranchial organ; pcl, *pharyngocleithrales* muscles; pf, pharyngobranchial folds; pfb, posterior (spongiose) fat body; pg pharyngobranchial groove; ppl, posterolateral articulatory process of 3rd pharyngobranchial; ppm, posteromedial articulatory process of 3rd pharyngobranchial; pt, proximal teeth; ptf, pterotic fat body; pv, posterior valve; rdd, *retractor dorsalis* muscle (dorsal section); rdv, *retractor dorsalis* muscle (ventral section); rem, *recti* muscles; rs, rudimentary sulcus; sa, sagitta; sb, sulcus border; SL, standard length; su, sulcus; swb, swimbladder; tp3, tp4, toothplates of pharyngobranchials 3 and 4; tps, strut of toothplate 4; tvs, *transversus* muscle; uh, urohyal; va, sulcal valve; vp, valve precursory folds.

STRUCTURE OF THE PHARYNGOBRANCHIAL ORGAN (PBO)

In those mugilids with a well-developed PBO, it occupies the rear of the pharynx and comprises two hemispherical 'denticulate' cushions. These cushions are separated from each other by a deep cleft in the ventral midline and are cupped ventrally and laterally by the branchial arches (Fig. 1). The relative size of the cushions is such that they occlude the narrow entrance of the oesophagus and, when the mouth is closed and the pharynx compressed, their ventral midline division is occupied by a strong septum joining the 5th ceratobranchials. When the mouth is opened and the buccal floor lowered the septum is withdrawn from between the denticulate cushions.

Externally the PBO comprises a posterolateral cushion formed of thick, stratified, epithelial tissue penetrated by numerous fine teeth (Plate ID & Fig.5C). The size of the cushion and the density of its tissue and teeth are interspecifically variable, but in most taxa the teeth along the ventrolateral and anterior border of the cushion are larger than those on its posteromedial surface (see below). Capanna *et al.* (1974) described the structure of the mucosa as comprising a thick surface layer of stratified epithelium separated by a marked basal membrane from loose, fibrillar connective tissue forming the submucosa. The entire cushion, the pharyngobranchial teeth lying within it and the supporting pharyngobranchial toothplates were referred to by Capanna *et al.* (1974) as the *denticulate area*, a term adopted here (da, in Figures).

Anteriorly, the denticulate area is separated from the 1st gill-arch by a deep channel, the *sulcus* (su), the depth, width, dorsal extension and orientation of which varies between taxa. The rim of the sulcus, formed by the margin of the denticulate area is named the *sulcus border* (sb). Dorsally, the sulcus runs longitudinally and becomes restricted posteriorly into a narrow aperture (do) roofed by the overlying 4th epibranchial (p. 115 and Fig. 1A). The sulcus continues posteroventrally as the deep groove which separates the denticulate (pharyngobranchial) part of the PBO from the internal muscles and fat bodies (Fig. 1A-C). The fold of tissue forming the anterior border of the sulcus is often expanded ventrally into a large flap or *valve* (va). In some taxa there is a single valve large enough to occlude the lower entrance to the sulcus (Fig. 10); in others the valve occurs as a single, small flap halfway along the sulcus, as a pair of flaps, or as small, finger-like projections (Figs 15 & 18).

The aforementioned PBO features situated anterior to the denticulate area appear to correspond to the 'gustatory' and 'mucus secreting' parts of the organ referred to by Capanna *et al.* (1974). These authors mention that in *Liza ramada* two 'plicae' occur where the denticulate part superimposes on the gustatory part. These 'plicae' would seem to correspond to the structures we refer to as valves.

Two large, spongiose *fat bodies* lie medial to the epibranchials and form the core of the organ (Figs 1 & 2). The *anterior fat body* (afb) is between the 2nd and 3rd epibranchials and often surrounds the latter, is covered by the thin wall of the sulcus and in many specimens bulges outward forming a nodule extending into the sulcus. We are not sure whether this is an artifact of preservation or whether, in life, the fat body moves outward when the *levator internus*, which runs

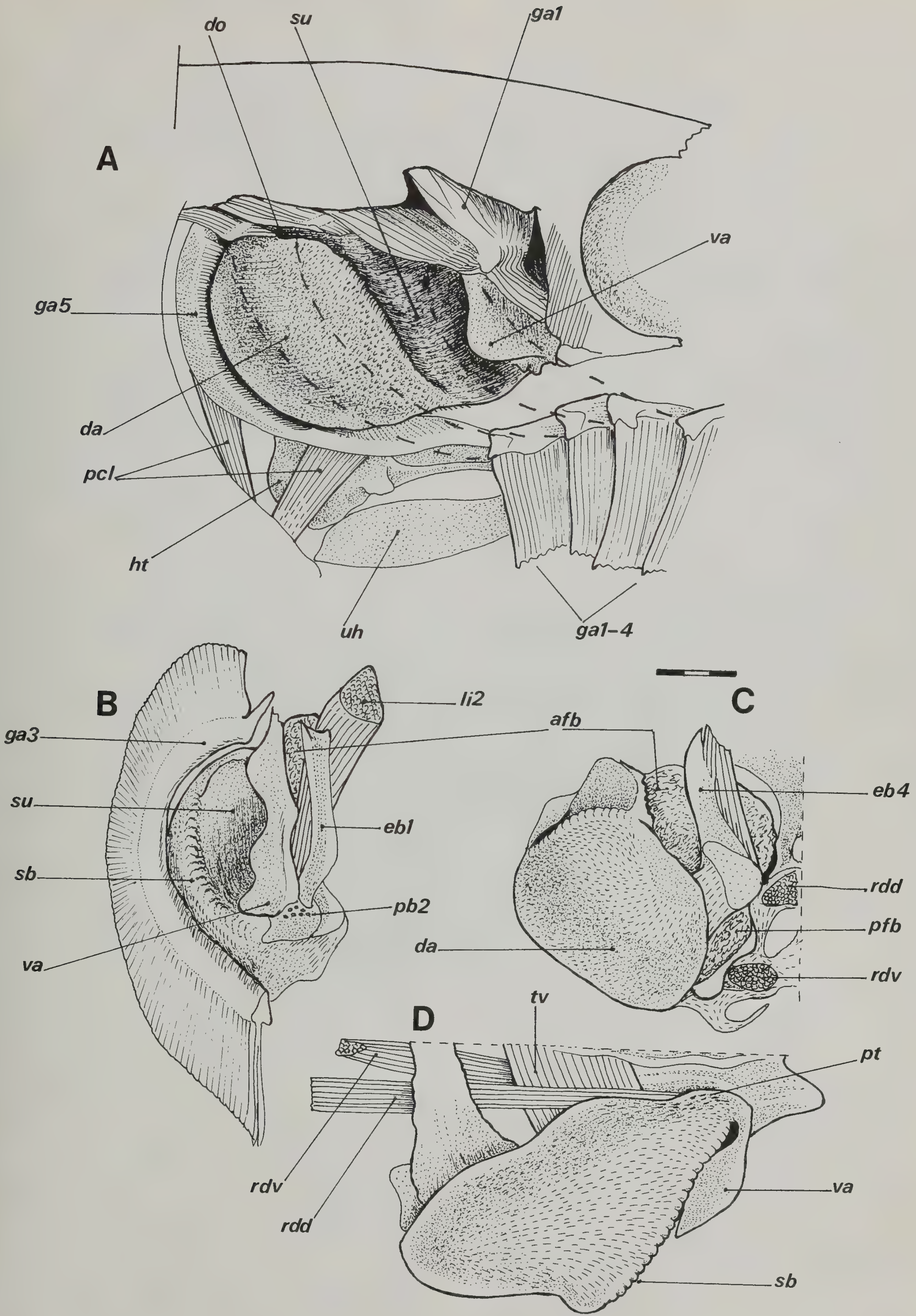
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Fig. 1 Position and structure of the mugilid pharyngobranchial organ (*Mugil* sp.). A, lateral view with gill-arches cut away, the dashed lines indicate the position of arches relative to the PBO. B, anterior view of right half of PBO, 1st and 2nd gill-arches have been removed. C, posterior, and D, ventral views of left half of PBO.

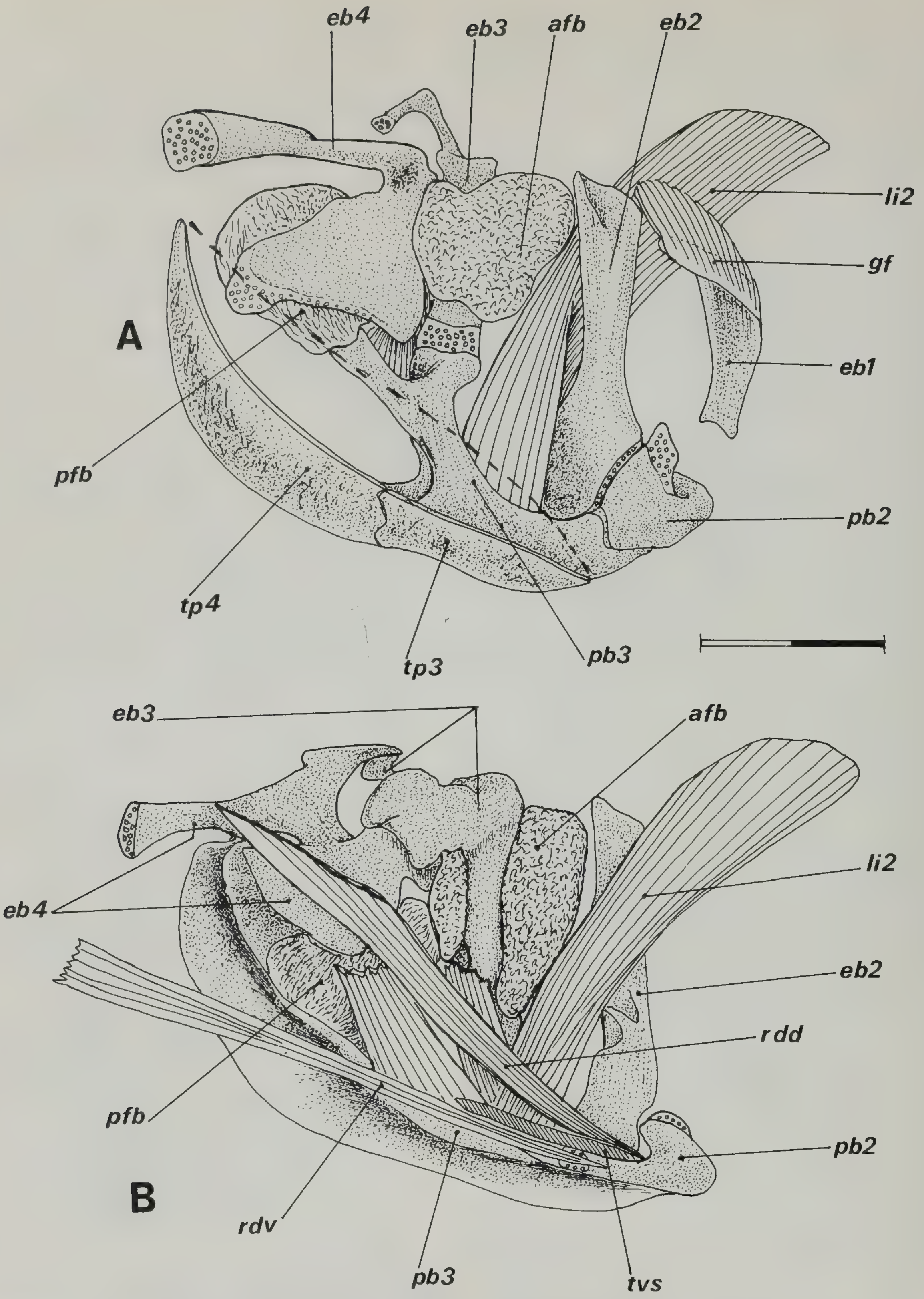

Fig. 2 PBO of *Liza ramada* (BMNH 1949.9. 16: 475–84, 99 mm SL). A, lateral view of right side, most of 3rd and 4th toothplates have been cut away, their dorsal margin shown by dashed line. B, medial view of left half; N.B., 3rd epibranchial surrounded by anterior fat-body.

anteromedial to it, is activated (p. 120). The more spongiose, *posterior fat body* (pfb) lies medial to the 4th epibranchial and a venous blood sinus passes through it.

The *principle muscles* which appear to be directly associated with the functioning of the PBO are the 2nd *levator internus* (li2) which connects the 3rd pharyngobranchial to the sphenotic (in all mugilids), and the *retractor dorsalis* which in the majority of mugilids is divided into distinct dorsal and ventral segments (Fig. 2). The dorsal section of the muscle (rdd) extends from the basioccipital and the ventral section (rdv) from the underside of the vertebral column (usually the 2nd centrum), with both sections inserting together on the 2nd pharyngobranchial (Figs 1C, D & 2B). In *Agonostomus* and *Joturus* the muscle retains its primitive condition as a single element, originating from the vertebral column, while in *Cestraeus* and *Aldrichetta* only some anterior fibres attach to the basioccipital. *Liza waigiensis* possesses an apparently unique condition in which the dorsal segment of the *retractor dorsalis* originates from a dorsally directed process of the 3rd neural spine (Fig. 3).

The *skeletal framework* of the PBO (Fig. 4) is provided principally by enlarged 3rd pharyngobranchial and 3rd and

4th toothplates; the 4th toothplate is posterolaterally extended to form a long, ventrally convex lamina. Both pharyngobranchial 3 and toothplate 4 are triangular and even in fry of *ca.* 15 mm SL are firmly united in tandem so forming a continuous structure (Fig. 6). The 3rd pharyngobranchial element consists of a fenestrated base-plate to which is attached a large toothplate (Figs 4 & 6). A longitudinal keel (pbk) rises dorsally from the plate to contact anteriorly the 2nd pharyngobranchial and dorsally the 2nd epibranchial. Posteriorly the keel deepens and broadens into two articular processes separated by a foramen in the bone. The medial process (ppm, Fig. 6) extends as a dorsoposterior strut, terminating in an outwardly facing articular head which contacts both the cartilaginous 4th pharyngobranchial and the base of the 4th epibranchial. The lateral process (ppl, Fig. 6) is a vertical pedestal with a flat surface articulating with the base of the 3rd epibranchial. The anterior border of the 4th toothplate rises as a thin, triangular lamina (tps, Fig. 6) adpressed to the inclined strut and vertical pedestal of the respective medial and lateral processes of the 3rd pharyngobranchial. The angles and posterior extent of the lateral and medial processes, and the degree of contact with the border of the 4th toothplate vary within the family.

Two types of *teeth* are associated with the pharyngobranchial toothplates: (1), those similar to the pharyngeal teeth of many other acanthopterygians in being separated from the supporting bone by a narrow collar of poorly mineralised bone (corresponding to the area of collagen described by Fink (1981) as diagnostic of his Type 2 attachment mode). These are referred to as *proximal-type* pharyngeal teeth (pt, Plate IA, C & Fig. 5A, B); (2), those in which the tips are distinctly separated from the bone, being borne on long, poorly mineralised shafts so that the tip of the tooth lies level with, or just below the surface of the epithelial cushion. These are referred to as *distal-type* pharyngeal teeth (dt, Plate IB, C & Fig. 5C).

The size and frequency of both types of teeth undergo considerable ontogenetic change (Capanna *et al.*, 1974; also below). In those taxa which lack a complex PBO (eg., *Agonostomus*, *Joturus*, *Cestraeus*, *Aldrichetta*), only proximal-type teeth are present. Furthermore, in these taxa pharyngobranchial 2 also bears such teeth (Fig. 5A; Rosen & Parenti, 1981: fig. 4C). The adults of those taxa with well-developed PBO's, in contrast, appear to lose most traces of proximal-type teeth but have well-developed distal-type dentition (Plate IC & D).

The following descriptions of teeth are based on juveniles of *Liza saliens*, *L. aurata*, *L. ramada* and *Chelon labrosus* of 40–80 mm SL from the Mediterranean. Although some interspecific differences exist (Drake *et al.*, 1984), the taxa have comparable dental ontogenies.

Proximal-type teeth occur only on pharyngobranchial 2 (in the adults of a few genera (Fig. 5A) and the juveniles of all others, pp. 115 & 119) and in a narrow band along the median borders of the 3rd and sometimes the anterior part of the 4th pharyngobranchial toothplates. The tips are either ankylosed directly with the plate or narrowly separated from it by a ring of poorly mineralised bone. Distal-type teeth cover greater parts of both toothplates. Each tooth is a long stem or shaft of poorly mineralised bone containing a cavity and terminating in a curved calcified tip which lies proud with the epithelial tissue of the mucosa covering the toothplate surfaces. The structure of the teeth varies both ontogenetically (Capanna *et al.*, 1974; also below) and spatially over the toothplates (Drake *et al.*, 1984). Those distal teeth closest to the medial border of the toothplate are relatively short compared with those situated more laterally. The latter are sequentially longer, with more highly calcified tips. (This size gradation is visible in micrographs of *Oedalechilus labeo*; Plate IC & D). However, distal teeth situated on the dorsolateral aspect of the plate are short and lack calcification. Although for the most part the shafts of the distal-type teeth are poorly mineralised, those on the lateral faces of the toothplates have well-ossified bases.

Drake *et al.* (1984: fig. 11) illustrated the directions in which the tips of the distal teeth curve with respect to their positions on the toothplates. Our observations are in agreement in that the teeth tend to form dense swathes with their tips all pointing in the same direction over various regions of the epithelial surface (see Plate ID for this pattern in *Oedalechilus labeo*). However, we observed greater variability in the directions of curvature than shown by Drake *et al.* The anterior teeth tend to have their tips curved anteriorly whereas those on the anterolateral part of the plate curve more anterolaterad and less mesad than shown by Drake *et al.* The posterior teeth tend to curve posteriorly rather than anteriorly.

Capanna *et al.* (1974) documented the tooth types in *Liza ramada*. Their terminology is somewhat confusing, however, when distinguishing between 'juvenile' and 'adult' teeth. The transverse sections through the denticulate cushions (Capanna *et al.*, 1974: figs 5 & 9) show distal teeth at various developmental stages or from different areas of the toothplates. In SE micrographs of the PBO of a juvenile fish (Capanna *et al.*, 1974: figs 12 & 13) the 'adult' teeth to which the authors refer appear to be proximal teeth (they are relatively robust and distributed in a narrow band along the medial borders of the toothplates).

In all taxa examined the 1st and 2nd *pharyngobranchials* are small elements (Figs 4 & 7). The 1st is a rod-like structure lying above the 2nd and sloping backwards with its anterior tip contacting the proximal cartilage of the 1st epibranchial. The 2nd, sometimes bearing proximal-type teeth, is an almost cuboid element abutting the 3rd pharyngobranchial and forming the anteroventral tip of the PBO; the *retractor dorsalis* attaches to it. An interarcual cartilage lies between the 1st and 2nd epibranchials (Fig. 7; also Travers, 1981: fig. 4).

The *epibranchials* are, with the exception of the 1st, complex structures with medial expansions which form the inner wall of the PBO. There is a good deal of intrafamilial variability in epibranchial morphology; for example, compare *Mugil* (Fig. 4) with *Liza* (Fig. 7).

The 1st epibranchial is nearly always slender and flat, inclined at 45° to the vertical and expanded distally where it articulates with the 1st ceratobranchial. The epibranchial bears an uncinate process which in *Mugil* (Fig. 4) is small and blunt, but which in *Liza* (Fig. 7) and *Chelon* is extended and triangular. Medially, the 2nd-4th epibranchials curve steeply ventrad to meet the pharyngobranchials. The 2nd epibranchial is usually scythe-shaped where it contacts the dorsal keel of the 3rd pharyngobranchial. Arising dorsally from the 3rd and 4th epibranchials are large, knuckle-like uncinate processes, that of the 3rd closely opposing that of the 4th (Figs 4 & 7). Epibranchials 3 and 4 articulate basally with the lateral and medial processes of the 3rd pharyngobranchial. The lateral shaft of the 4th epibranchial bridges the posterodorsal rim of the sulcus, and so forms the narrow, tunnel-like dorsal

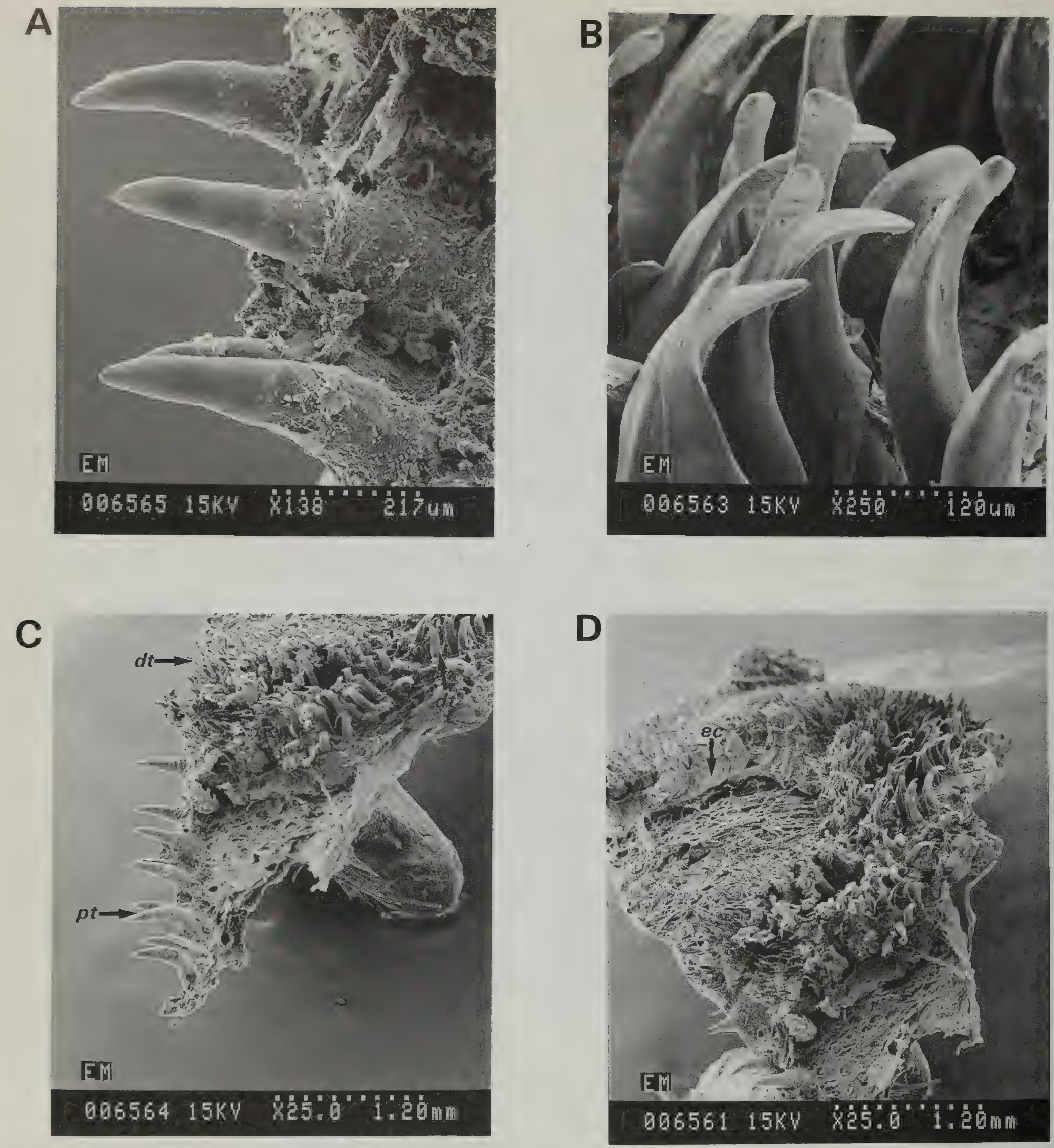

Plate I Scanning electron micrographs of denticulate area of *Oedalechilus labeo* (BMNH 1947.11.2: 1–10, 157 mm SL). A, proximal-type teeth in ventrolateral view; B, distal-type teeth in anteroventral view; C, anterior part of denticulate area in ventrolateral view. Note narrow band of proximal teeth on medial edge, and size gradation of distal teeth from largest situated laterally (arrowed, top-right) to smallest medially (arrowed, top centre); D, entire denticulate area in anteroventral view. Note extensive coverage by various swathes of distal teeth with tips pointing in similar directions, and size gradation from lateral teeth (on right side) to medial teeth (left side). Large central area damaged and devoid of teeth, posterior to this the thick mucosa of the epithelial cushion in which the distal teeth are embedded is visible (arrowed). Scale bars are shown at base of each micrograph.

aperture of the sulcus (Fig. 1A). The 1st and 2nd epibranchials are widely separated from the 3rd and 4th.

The 1st epibranchial bears long gill-rakers on its leading edge and these, in turn, bear small lateral lamellae projecting towards, if not interdigitating with those of the neighbouring outer rakers. Short rakers are present on the distal part of the 1st epibranchial's inner margin, extending to a point level with the uncinate process. There are no gill-rakers on the other epibranchials.

The *ceratobranchials* are long; the 1st bears long outer

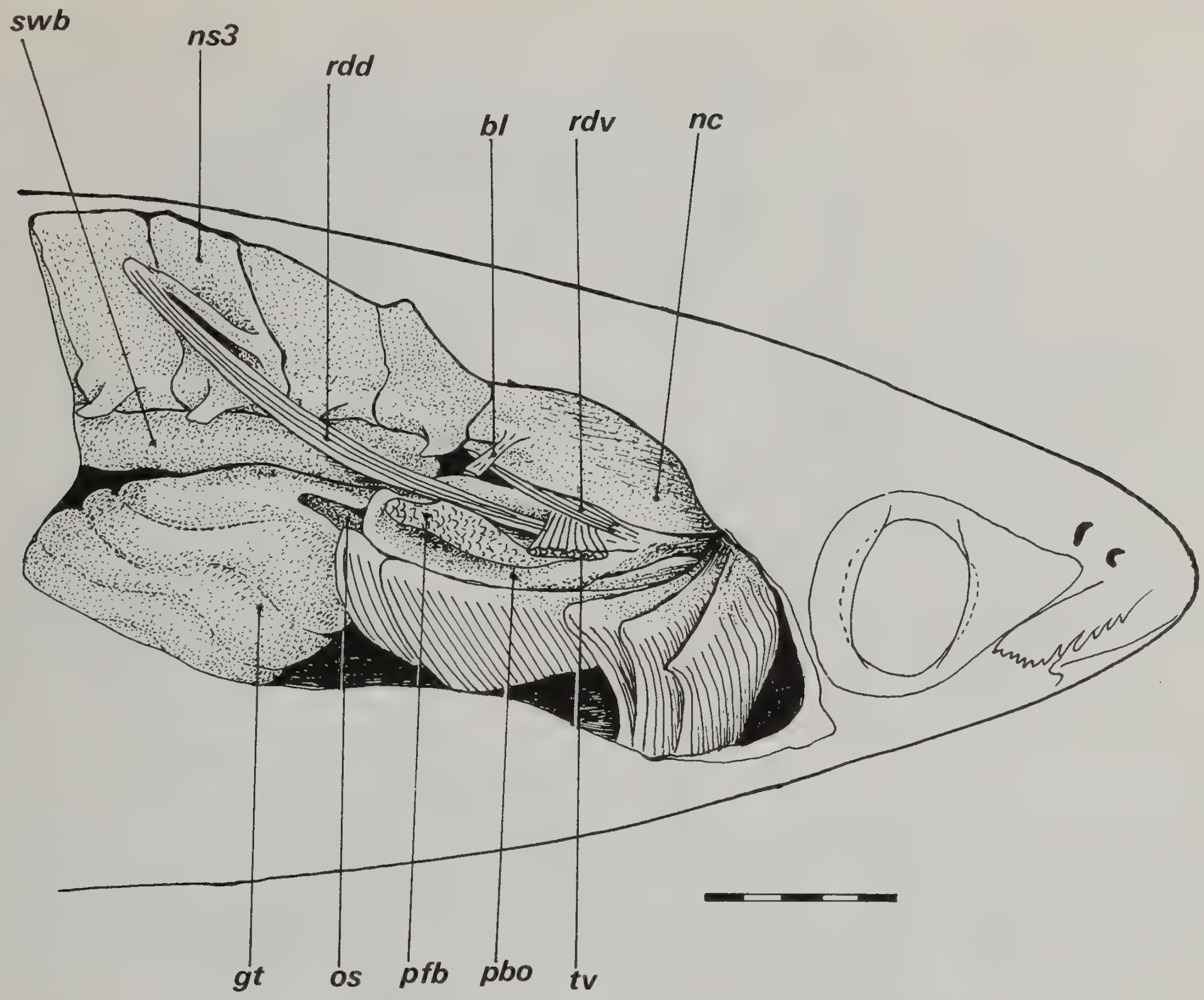

Fig. 3 *Liza waigiensis* (BMNH 1974.5. 25: 3649–73, 97 mm SL). Dissection of head to show unique configuration of *retractor dorsalis* muscle; the right half of the PBO has been cut away.

gill-rakers similar to those on the 1st epibranchial, and lies well anterior to the denticulate area of the PBO. The 2nd and 3rd ceratobranchials have shorter and closer-set gill-rakers and lie anterior to the PBO, although the posterior rakers of the 3rd surround part of the sulcus border. The 4th ceratobranchial surrounds the lateral face of the denticulate area, and the 5th, which is an expanded lamniform bone, cups the posteromedial region of the organ. The medial border of the 5th ceratobranchial bears proximal-type teeth which are distinct in the juveniles but remain relatively small, if not vestigial, in adults (p. 119). The gill-rakers on the inner surfaces of the ceratobranchials are spaced and orientated in such a way that when drawn together, they intermesh with the outer rakers of the next arch. Since the gill-rakers of the 4th and 5th ceratobranchials enclose the denticulate cushion, they intermesh with the distal teeth of the organ. Several types of gill-raker can be recognised in mugilids (Ingham, 1952). The cartilaginous tips of the 2nd-4th ceratobranchials, which articulate with those on the epibranchials, are drawn out into scytheshaped blades; from these run the rows of gill filaments which pass away from and above the epibranchials and are supported only by their transverse membrane (Fig. 7).

DEVELOPMENT

The following ontogenetic observations apply to *Mugil cephalus*, *Liza saliens*, *L. aurata*, *L. ramada* and *Chelon labrosus* from the Mediterranean.

External morphology: The PBO is at least moderately developed in specimens of *ca*. 11 mm SL. *Liza* spp of this size have folds on the anterior part of the lateral wall which are the precursors of the valves characteristic of adult PBOs and are referred to as *valve precursors* (VP). There is a short-based VP anteroventrally, which is not always distinct, and a long-based VP posteriorly. Both are moderately papillate but neither projects prominently from the wall of the PBO; indeed the posterior VP covers and lies flush within the narrow sulcus. The posterior VP of *Liza* and *Chelon* appears to be homologous with the single long-based VP of *Mugil*. In *Mugil cephalus* of 14.5 mm SL the single fold is distinct and the sulcus is relatively broad, unlike the condition in *Liza* of the same size. In *M. cephalus* above 15 mm SL the transition from VP to adult valve involves little modification, the fold merely becomes proportionately larger and more distinct, particularly in specimens above 20 mm SL. In *Liza* of 15–20 mm SL the VPs also enlarge but the anterior fold remains relatively small and the sulcus narrow (Fig. 8A). In *Chelon* of the same sizes both VPs are large and bulbous and the sulcus is broader (Fig. 8B).

Between 20–34 mm SL the VPs in *Liza* and *Chelon* undergo further changes. The anterior VP becomes more fleshy and prominent but retains its shorter base. In *Chelon labrosus* and *Liza saliens* of *ca*. 33 mm SL the anterior valve has an accessory process, which in *L. saliens* of *ca*. 50 mm SL develops into an elongate flap. The posterior VP becomes distinctly triangular but the transition to its final form varies between taxa. In *C. labrosus* and *Liza aurata* the valve remains long-based, large and fleshy; in *L. ramada* the

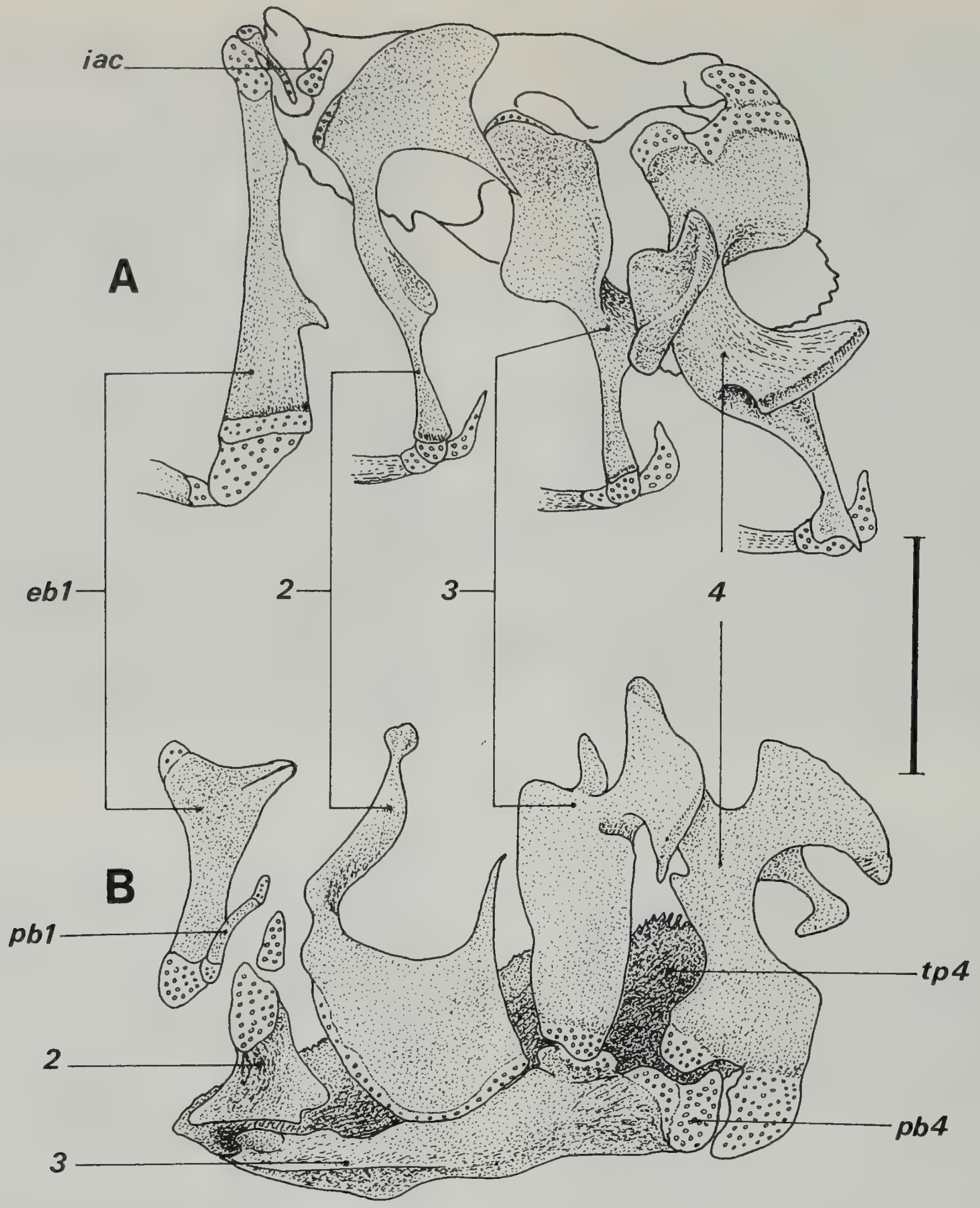

Fig. 4 Upper gill-arch elements of *Mugil cephalus* in A, dorsal and B, medial views. For clarity, in A, the toothplates are shown in outline only. Specimen PA 271186T, 27.5 mm SL. Scale = 0.5 mm.

ultimate structure is a small protruberance, the original long fold remaining as its fleshy base. Between 30–44 mm SL these three taxa also develop a secondary valve or protruberance from the ventral part of the posterior VP. The sulcus is present in the earliest available stages as a narrow and shallow groove. The principal changes in its morphology occur between *ca*. 23–40 mm SL and involve increases in breadth and depth. The most significant development is the opening and widening of the dorsoposterior aperture beneath the 4th epibranchial (Fig. 1A).

Skeletal elements: Discounting intergeneric and interspecific variability in the adult form, the basic ontogeny of the upper gill-arch elements follows the same pattern in all taxa studied. At the earliest available stage (12.5 mm SL *Liza ramada*, Fig. 9A), the toothplates are triangular and meet one another along their respective straight, posterior and anterior borders, The 4th toothplate is shorter than the 3rd and both bear a few proximal-type teeth mostly along their outer margins. Along its posterior border the 3rd pharyngobranchial bears two small cartilaginous processes; a lateral one articulating with the 3rd epibranchial and a medial one articulating with the cartilaginous 4th pharyngobranchial which, in turn, articulates with the 4th epibranchial. The 2nd pharyngobranchial bears distinct proximal teeth.

In a 14 mm SL *Liza saliens* (Fig. 9B), the situation is similar but the articular processes have extended and a thin laminate keel has developed from the base of the lateral process to extend anteriorly. The base of the 4th epibranchial has expanded to overlap the 4th pharyngobranchial. The teeth are of the proximal type.

At 16–18 mm SL (Fig. 9C), the articular processes of the 3rd pharyngobranchial have developed substantially. A strong keel runs anteriorly from the base of the lateral process whose articular surface has become partially ossified. The anterior border of the 4th pharyngobranchial toothplate has developed a strong lip which abuts the lateral articular process of the 3rd pharyngobranchial. The base of the 4th epibranchial has expanded and nearly reaches the medial articular process of the 3rd pharyngobranchial. Differentiation of the pharyngeal dentition is apparent at these stages; laterally the 4th toothplate bears teeth intermediate in length and thickness between proximal and distal morphotypes. In a 16.5 mm SL *Mugil cephalus*, and at subsequent stages, teeth are absent from the 2nd pharyngobranchial.

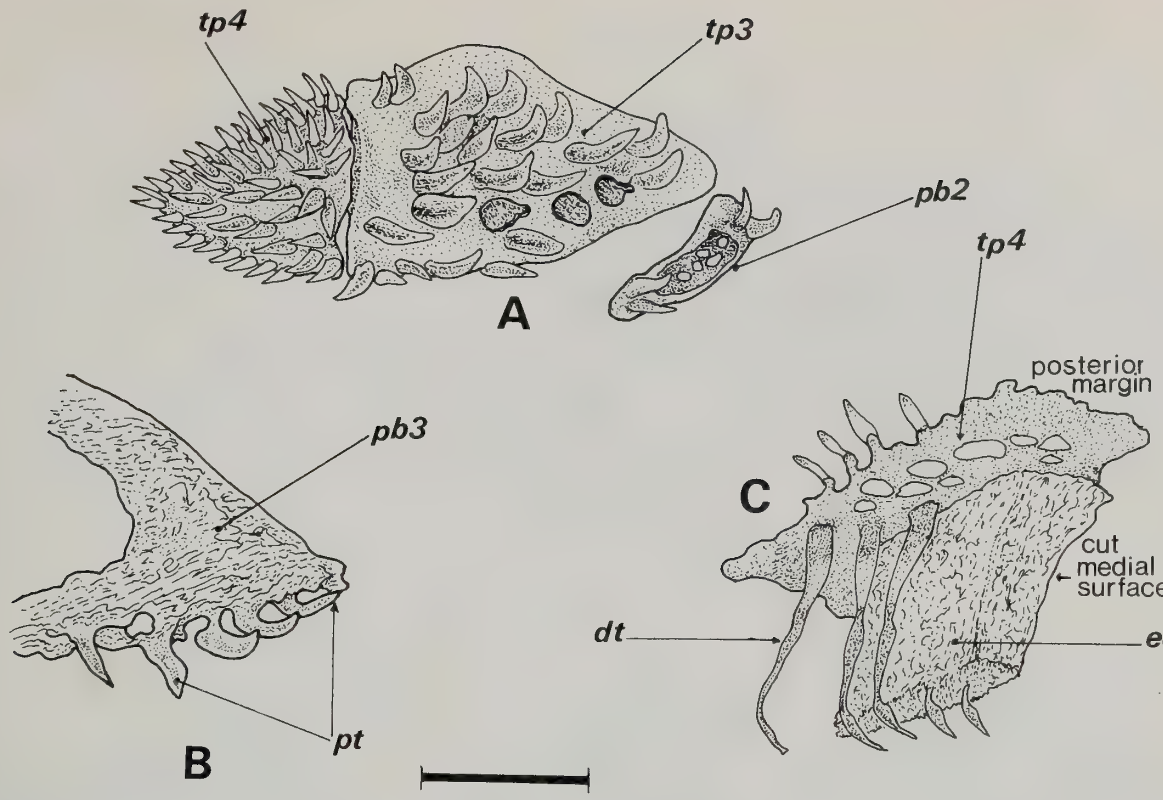

Fig. 5 Pharyngobranchial teeth in A, *Agonostomus* sp. (BMNH 1985.3. 18: 22–37, *ca.* 35 mm SL), ventral view of toothplates, all teeth are of the proximal-type. B & C, *Chaenomugil proboscideus* (BMNH 1903.5. 15: 278–9, 56 mm SL); B shows anterior tip of pharyngobranchial 3 bearing proximal-type teeth; C shows part of a row of distal-type teeth on pharyngobranchial 4 toothplate, the epithelial cushion has been cut away to expose entire shafts of lateral teeth. N.B., teeth stemming from the free lateral margin of the toothplate. B & C viewed ventrolaterally. Scale = 0.5 mm.

At 19–23 mm SL the skeletal elements, including the core of the 1st pharyngobranchial, are well ossified. The dorsal keel of the 3rd pharyngobranchial and the lateral and medial articular processes of both the 3rd pharyngobranchial and 4th toothplate enlarge. The anterior lip of the 4th toothplate elevates to contact the surface of the lateral articular process rising from the 3rd pharyngobranchial. The teeth are characteristically of the distal-type on the lateral part of the 3rd pharyngobranchial toothplate and entirely so on the 4th which expands and lengthens to more than half the length of the 3rd.

At 28 mm SL the 4th toothplate is distinctly broadened and its length usually equals that of the 3rd. Both are covered principally by distal-type teeth although a few proximal-types may remain on their medial borders. At a later stage (36 mm *L. saliens*, Fig. 9D) the adult pharyngobranchial characteristics are developed. The lateral process, articulating with the 3rd epibranchial, is now positioned centrally due to the lateral expansion of the toothplate. The 'lip' of the 4th toothplate border is now a thin lamina adpressed to the lateral and part of the medial processes of the 3rd pharyngobranchial. Later, as the medial process extends further posteriorly, the dorsal lamina of the 4th toothplate makes more extensive contact with it and presumably aids its support. The 2nd pharyngobranchial bears one or two 'intermediate-type' teeth (see above). At *ca.* 30 mm SL and above the 2nd pharyngobranchial is edentulous in all taxa examined.

The 5th ceratobranchial appears slender in the smallest specimens examined and it bears proximal-type teeth. During ontogeny this ceratobranchial expands anterolaterally to oppose the developing 3rd and 4th pharyngobranchial toothplates. The proximal teeth become restricted to a narrow band on the medial border of the 5th ceratobranchial in fish of *ca.* 30 mm SL. At later stages these teeth appear progressively less distinct and eventually vestigial.

POSSIBLE MODE OF FUNCTION OF THE PBO

Information on the function of the PBO is lacking but in previous descriptions of the organ it has been hypothesised to play an important sensory and mechanical role in the sampling and filtration of the water currents laden with food material (Odum, 1968; Capanna *et al.*, 1974; Ching, 1977; Drake *et al.*, 1984). Having studied the gross and microanatomy of the PBO in *Liza ramada*, Capanna *et al.* (1974) arrived at a functional hypothesis which depends on there being a narrow and restricted buccopharyngeal cavity preventing entry of large particles into the gut. They supposed that the denticulate area, nested within the branchial basket, provides the mechanical factor in food particle selection (see below), whereas they assumed that the sulcus (which they termed the 'gustatory region') acts as a chemical sampler.

We agree with the basic functional hypothesis of Capanna *et al.*, but surmise that the sulcus plays a more active role as the principle flow channel for the particle-laden water, as well as being a sampling area. The role of the valve(s) is more difficult to determine. Capanna *et al.* (1974) considered them to be sites of mucus production, but disparity in size and shape also suggests a role as water-current controllers. In *Mugil cephalus*, for example, when 'closed' the valve almost occludes the entrance to the sulcus (Fig. 10).

We suggest that the particle-laden water current is initially directed up the sulcus where it is chemically sampled. If found

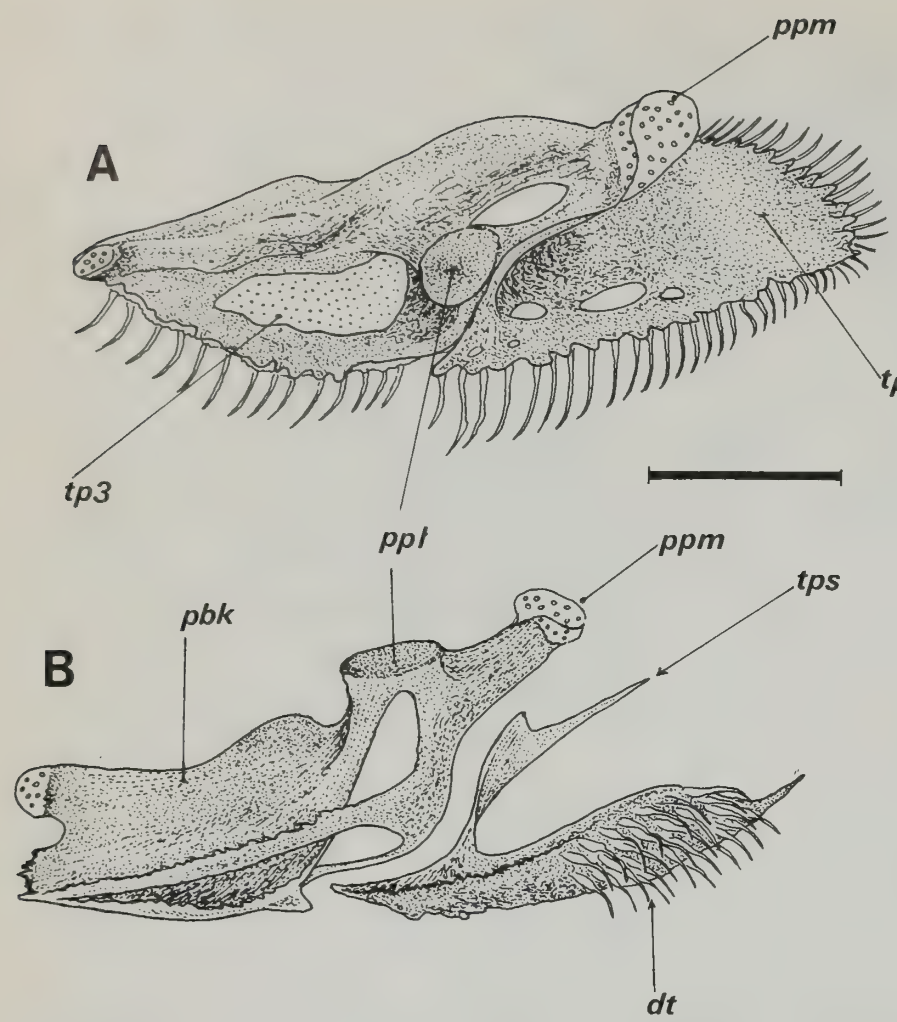

Fig. 6 3rd & 4th pharyngobranchials and toothplates of *Mugil cephalus* (PA 271186T, 27.5 mm SL) in A, dorsal and B, lateral views. In B, the 4th toothplate has been separated from the 3rd pharyngobranchial to show detail of opposing surfaces. For clarity, the 3rd toothplate has been removed from its supporting bone and only a few distal teeth are shown on toothplate 4. Scale = 0.5 mm.

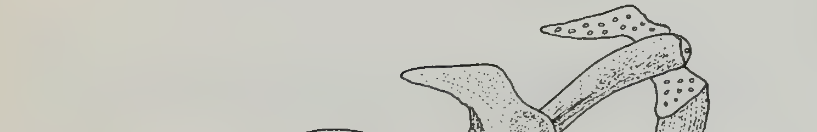

Fig. 7 Upper gill-arch elements of *Liza ramada* (PA 17986T, 57.5 mm SL). Gill-filaments are shown extending from the 2nd ceratobranchial process to above the uncinate process of the 2nd epibranchial. Scale = 0.5 mm.

suitable for filtering the current is then forced over the sulcus border and filtered across the denticulate area. Small corrugations along the border possibly aid in channelling and altering the nature of the flow of the current as it is ejected from the sulcus. The mechanism of ejection is most likely achieved through elevation of the pharyngobranchial unit by the *levator internus* 2, an action which might also displace the anterior fat body outwards, thus sealing the sulcus dorsally.

According to Capanna *et al.* (1974) the particle-laden current passes between the denticulate area and the intermeshing rakers which prevent the passage of coarser material. The structure of the PBO indicates to us that it may be able to regulate its filtering capacity by adjusting the degree of separation between the denticulate area distal-type teeth and the gill-rakers. The larger distal-type teeth along the sulcus margin and lateral face of the denticulate area presumably serve to entrap the coarser material as do the anteromedial proximal-type teeth. Transport of the particulate matter to the oesophagus is possibly *via* streams of mucus emmanating from the valve area (Capanna *et al.*, 1974), Ojha & Mishra, (1987), report mucous gland openings at the base of the gill-rakers in *Rhinomugil*). Observations (eg., Günther, 1861; Hickling, 1970) indicate that sediment is worked for some time between the pharyngeal bones, implying that material is passed over the denticulate area more than once by a circulating current. Such a current would carry the mucus posteriorly to meet the filtrate behind the PBO (Fig. 11). It is noted that the oesophageal opening is not in the same horizontal plane as the buccal cavity but elevated to just beneath the vertebral column (Fig. 3).

According to *in vivo* observations of Capanna *et al.* (1974), the non-ingested particles are removed from the PBO by

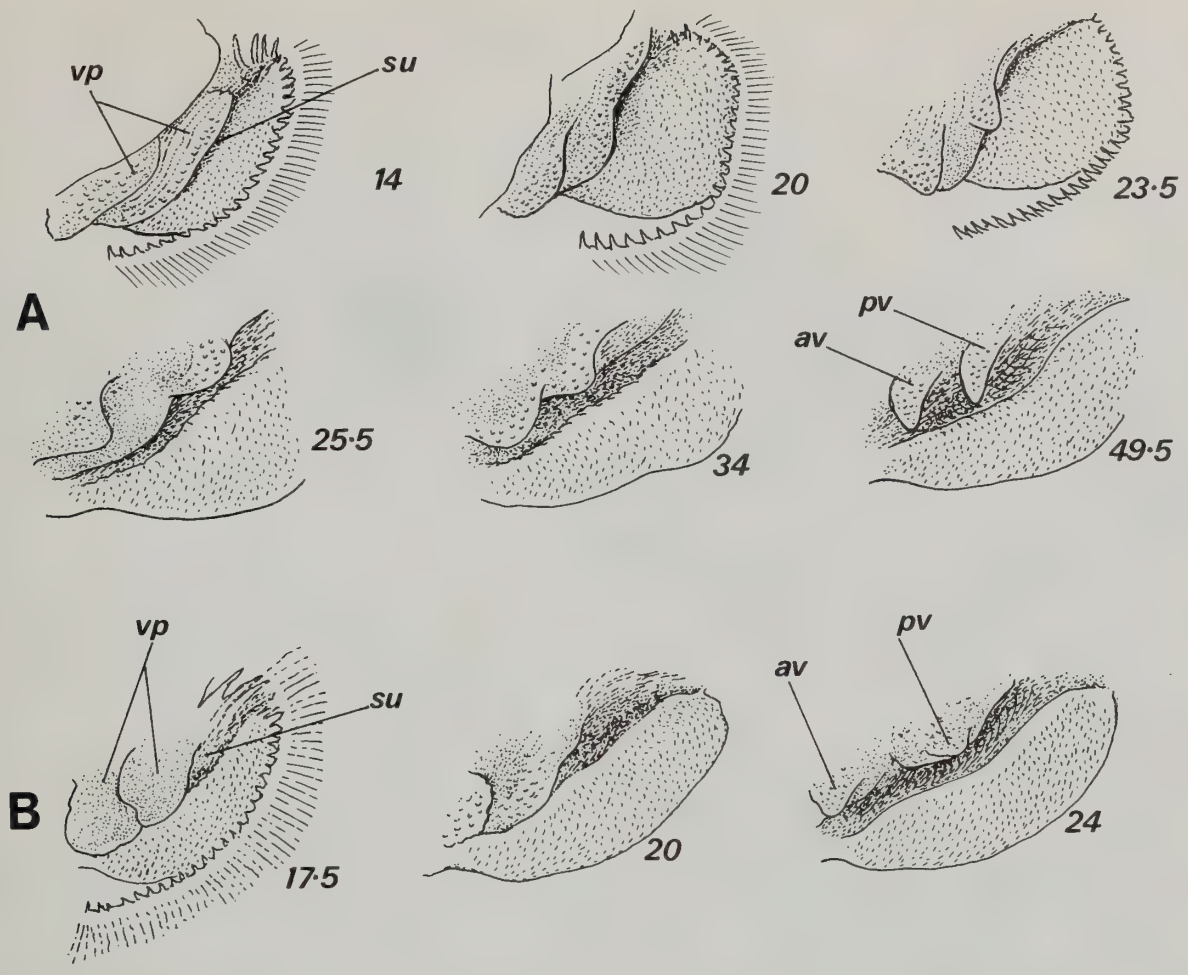

Fig. 8 Developmental series of the PBO in A, *Liza saliens* (PA 17986R) and B, *Chelon labrosus* (PA 19685R). First three figures in ventrolateral view, others lateral. Numbers indicate SL (mm).

'vibratory release movements imparted by the intrinsic muscles of the organ's denticulated valve' (*ie.*, *levator internus* 2 muscle). In this way the denticulated area is possibly agitated against the gill arch which would rake the mulch of particles off its surface. Any strands of detritus (*eg.*, filamentous algae) which became attached to the gill-rakers might be removed by the rakers of neighbouring ceratobranchials when these are drawn together and their rakers intermeshed (see above). In this way the gill-rakers' own close intermeshing might act as a self-cleaning mechanism. The non-ingested material is flushed out of the mouth (Günther, 1861; Hickling, 1970; Capanna *et al.*, 1974). The sulcus and its ventral valve may well contribute to the flushing process by directing the flow when the buccal cavity is evacuated.

The hypothesis that the sulcus, valves and denticulate area play important roles in the sampling and filtration of the water current passing over them is supported by simultaneous morphological and trophic changes during ontogeny. There is a certain amount of interspecific variability in diet as well as that related to locality and habitat (see below). Nonetheless, there is a consistent trend for mugilids to show a trophic shift from exclusive carnivory (taking neustonic zooplankton during postlarval stages) to ilyophagy in juvenile and adult stages (Ebeling, 1957; Thomson, 1966; Ching, 1977; also De Silva, 1980 and Brusle, 1981 for literature reviews).

Mugilids usually assume the adult diet prior to 50 mm SL. Most previous work indicates that the principal dietary phase transition in fish occurs between 20–30 mm SL (Ebeling, 1957; Hickling, 1970; Albertini-Berhaut, 1973, 1974; Ching, 1977; De Silva & Wijeyaratne, 1977; Ceccherelli *et al.*, 1981; Ferrari & Chieregato, 1981; Tosi & Torricelli, 1989). Work by Blaber & Whitfield (1977) and Chan & Chua (1979) suggests that the dietary transition may even occur in fish of between 10–20 mm SL. The simple structure of the PBO during postlarval stages and the predominance of proximal-, rather than distal-type teeth both on the denticulate area and 5th ceratobranchial suggest the fish are better suited for the selection of planktonic items.

A functional hypothesis of the PBO should take into account mouth and buccal cavity morphology and movements. Such studies are beyond the scope of this survey but it may be mentioned that jaw and pharyngeal pouch teeth have a similar morphology and ontogeny. The upper and lower jaw teeth form from a thin lateral margin of bone (staining only with alcian blue at all growth stages), which becomes foraminated, fretted, and eventually shredded into the strands which form the tooth-shafts. Furthermore, there appears to be some correlation between lower jaw shape (ventral profile) and PBO morphotype (Fig. 19F). Marais (1980) and Drake *et al.* (1984) concluded that jaw tooth morphology is an important factor in determining diet. We note that the 'fringes' of jaw teeth in such forms as *Chaenomugil* and *Neomyxus* (Fig. 19A & B) possibly play a role in pre-oral selection.

TAXONOMIC SURVEY OF PBO

AGONOSTOMUS Bennett, 1832 (Fig. 12A): PBO absent; pharyngobranchial 3 orientated horizontally, with 2nd, and

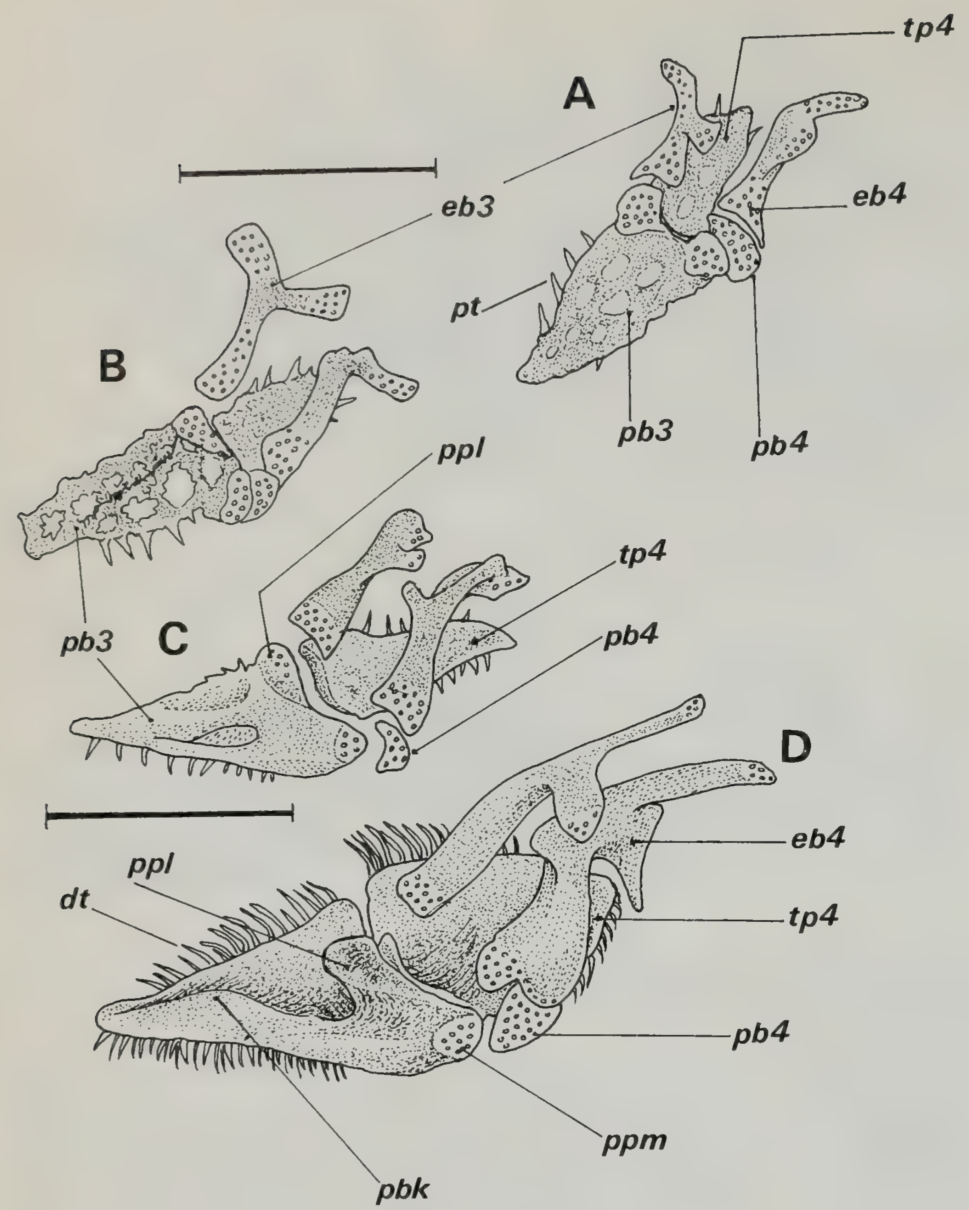
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Fig. 9 Developmental series of right pharyngobranchials and 3rd and 4th epibranchials in A, *Liza ramada* of 12.5 mm SL (PA 17986R), B-D, *Liza saliens* of 14, 18 (PA17986R) and 36 mm SL (PA281086R). A and B in dorsal, C and D in dorsolateral views. Scales = 1 mm.

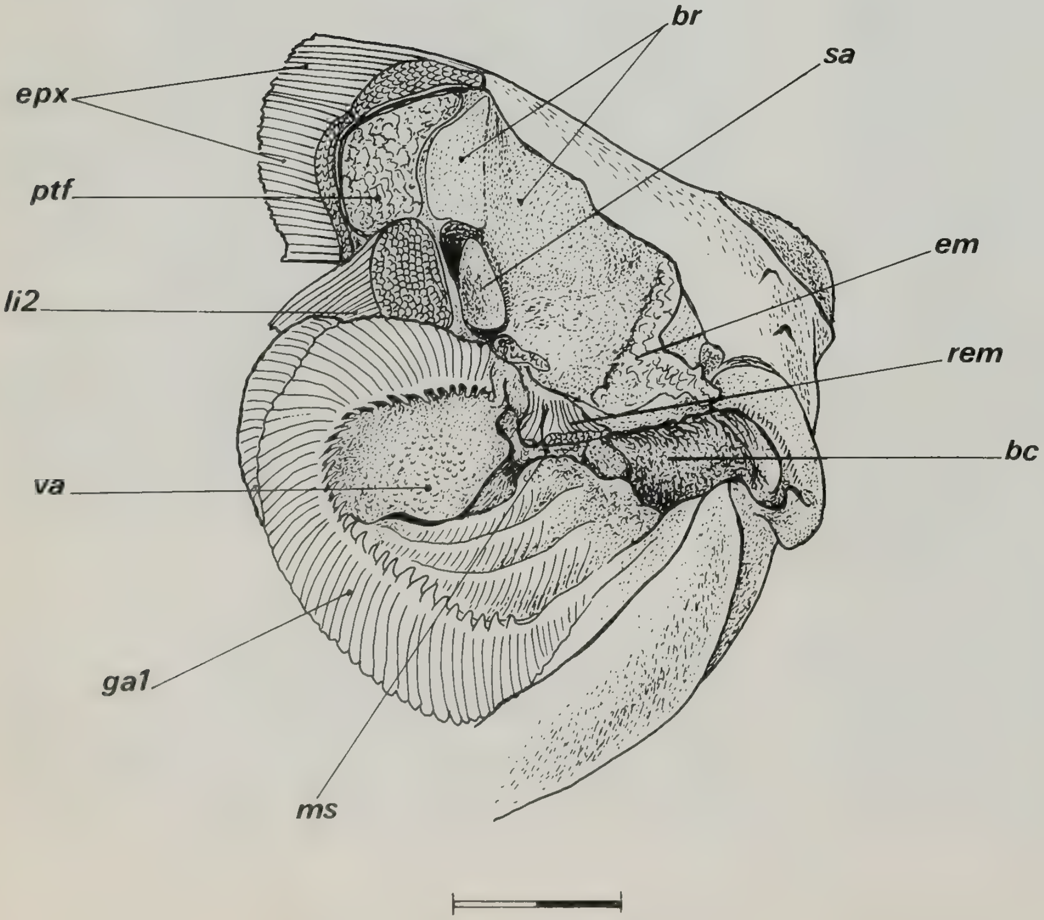
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Fig. 10 *Mugil cephalus* (PA 13386T, 48 mm SL). Oblique frontal view of dissected head showing buccal cavity and position of sulcal valve; the rakers of the 1st gill-arch crossing the valve have been cut, normally they extend across the front of it. Other features shown are muscles and fat bodies lying within the cranium.

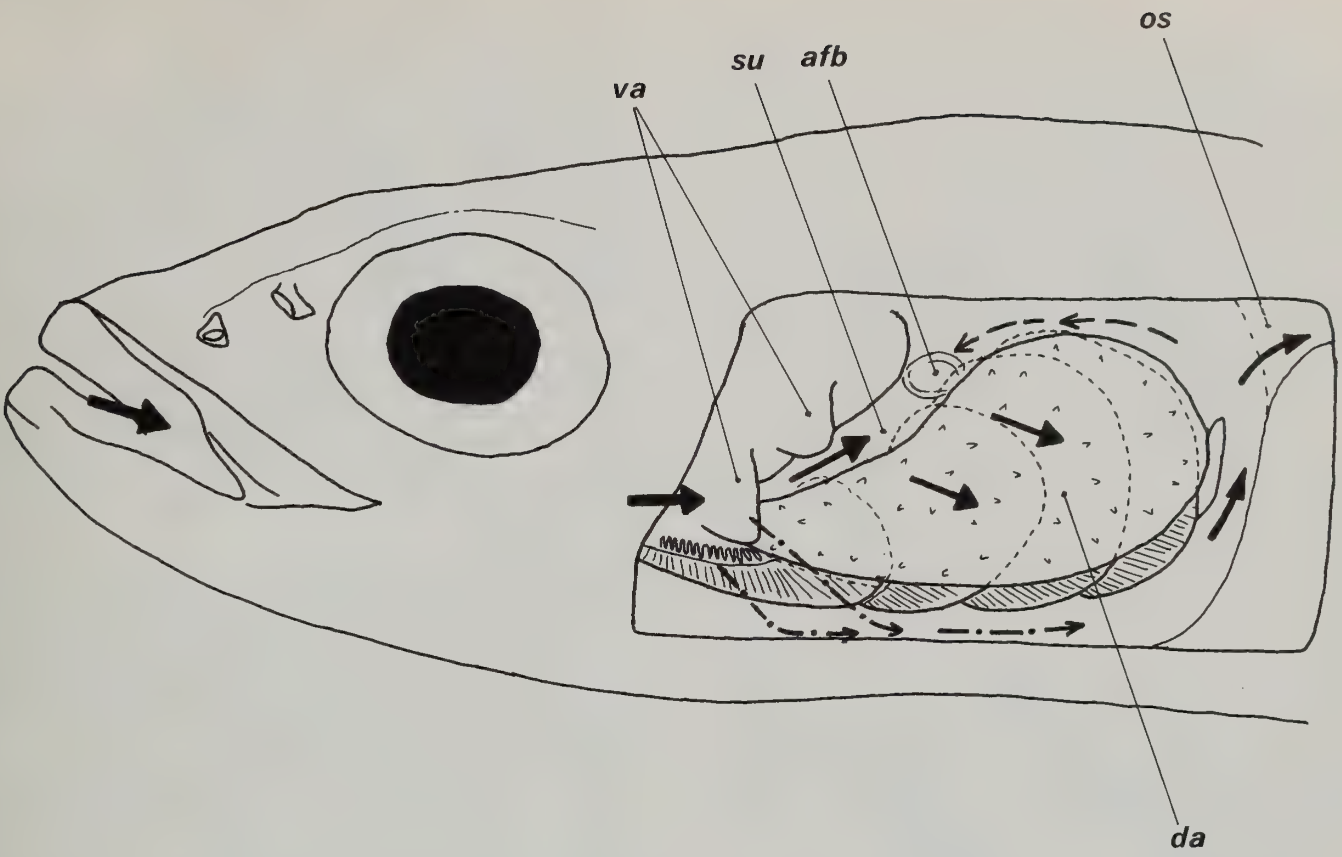

Fig. 11 Diagrammatic representation of hypothesised flow of food-laden water (thick arrow), filtered and recirculated water (dashed arrow), and mucus (dashed/dotted arrow) around PBO. The surrounding gill-arches are indicated by broken lines.

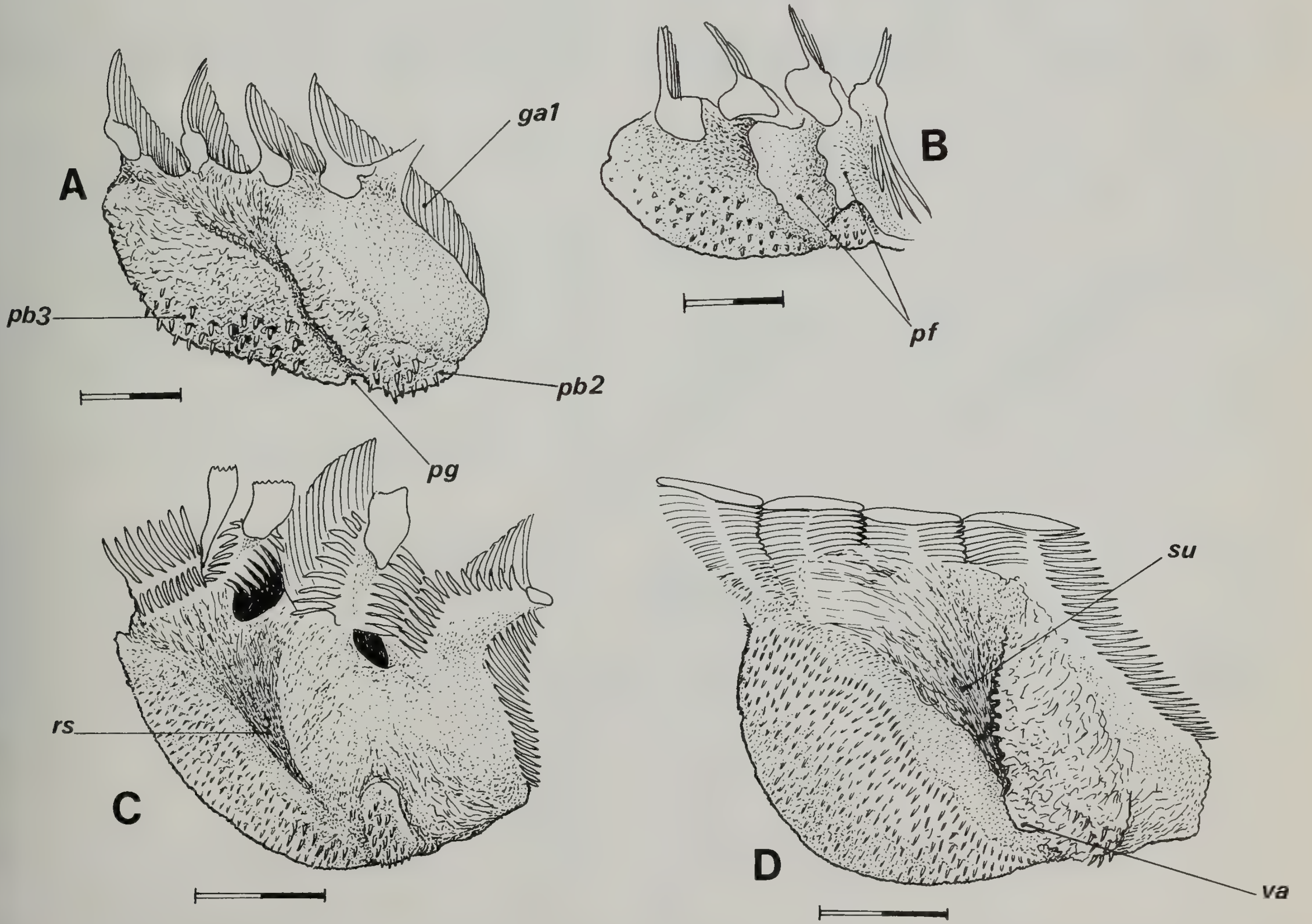

Fig. 12 PBO of A, *Agonostomus monticola* (BMNH 1985.3.18: 139–141, 127 mm SL); B, *Joturus pichardi* (1933.3.6: 199–204, 113 mm SL); C, *Cestraeus oxyrynchus* (1879.3.4: 1, 108mm SL); D, *Aldrichetta forsteri* (1899.2.14: 38–43, 178 mm SL). All in ventrolateral view of right side.

3rd and 4th toothplates bearing strong, downwardly pointing (proximal) teeth (Fig. 5A). Thick epidermal tissue surrounds toothplates and proximal portions of epibranchials, forming 'pharyngeal pads' which are widely separated across the midline. Condition similar in both species examined, *A. telfairii*, *A. monticola*.

JOTURUS Poey, 1860 (Fig. 12B): PBO absent; upper pharyngeal morphology similar to that of *Agonostomus* but with two loose folds of tissue covering the area between the 2nd and 3rd pharyngobranchials. When the fold covering the anterior border of toothplate 3 is lifted, a rudimentary sulcus is exposed.

CESTRAEUS Valenciennes, 1836 (Fig. 12C): PBO rudimentary; pharyngeal morphology similar to that of *Joturus* but lacking folded tissue; although a rudimentary sulcus is present, that of *C. oxyrynchus* and *C. plicatilis* (type species) is deeper and more well-defined than that of *C. goeldii*.

ALDRICHETTA Whitley, 1945 (Fig. 12D): PBO morphology intermediate between *Cestraeus* and more advanced mugilids; sulcus V-shaped, narrow and shallow. Teeth on pharyngobranchial 2 and medial teeth on 3, of proximal-type, outer teeth and all those on 4th toothplate are of distal-type. Tissue anterior to sulcus highly convoluted and papillose, covering a medial fat body between 2nd and 3rd epibranchials. Pharyngobranchial pads broadly separated by deep furrow.

MYXUS Günther, 1861 (Fig. 13A): PBO developed; denticulate area large with broadly convex sulcus border; cushions deeply divided; sulcus wide, diagonal; valve in form of a double papillose pad. Of the included species, *M. elongatus* (type species) and *M. petardi* closely resemble one another but *M. capensis* has a PBO morphology which more closely resembles that of *Mugil cephalus* (p. 125).

SICAMUGIL Fowler, 1939 (Fig. 13B): PBO with shallow denticulate area, sulcus border almost straight; sulcus diagonal, wide and shallow; single large valve situated anteroventrally, its anterior border infolded forming a pocket. Denticulate cushions widely separated by a ridge which expands anteriorly into a conical structure lying between the lateral valve-pockets.

RHINOMUGIL Gill, 1863 (Fig. 15D): PBO with moderate denticulate area, straight sulcus border bearing a row of prominent papillae; sulcus diagonal, rather broad, a well-developed valve at lower end which has a papillate inner surface. Teeth are exceptionally fine and hidden in mucosa; those along the sulcal margin only slightly enlarged, as are the proximal teeth.

NEOMYXUS Steindachner, 1878 (Fig. 14A): PBO with extensive denticulate area; teeth arranged in transverse rows, those along sulcus border and over dorsoanterior area setiform; cushions widely separated posteriorly, a transverse papillose septum anteriorly; sulcus deep, vertical and narrow, with a tripartite valve at lower end.

CHAENOMUGIL Gill, 1863 (Fig. 14B): PBO with reduced denticulate area; cushions deeply divided, teeth arranged in regular rows, those along sulcus border setiform; sulcus border markedly concave; sulcus extensive, no valves.

CHELON Röse, 1793 (Fig. 14C): PBO with denticulate area relatively large, cushions deeply divided, posterolateral distal-type teeth of almost even size, those anteroventrally longer and anteriorly curved; sulcus border slightly corrugated

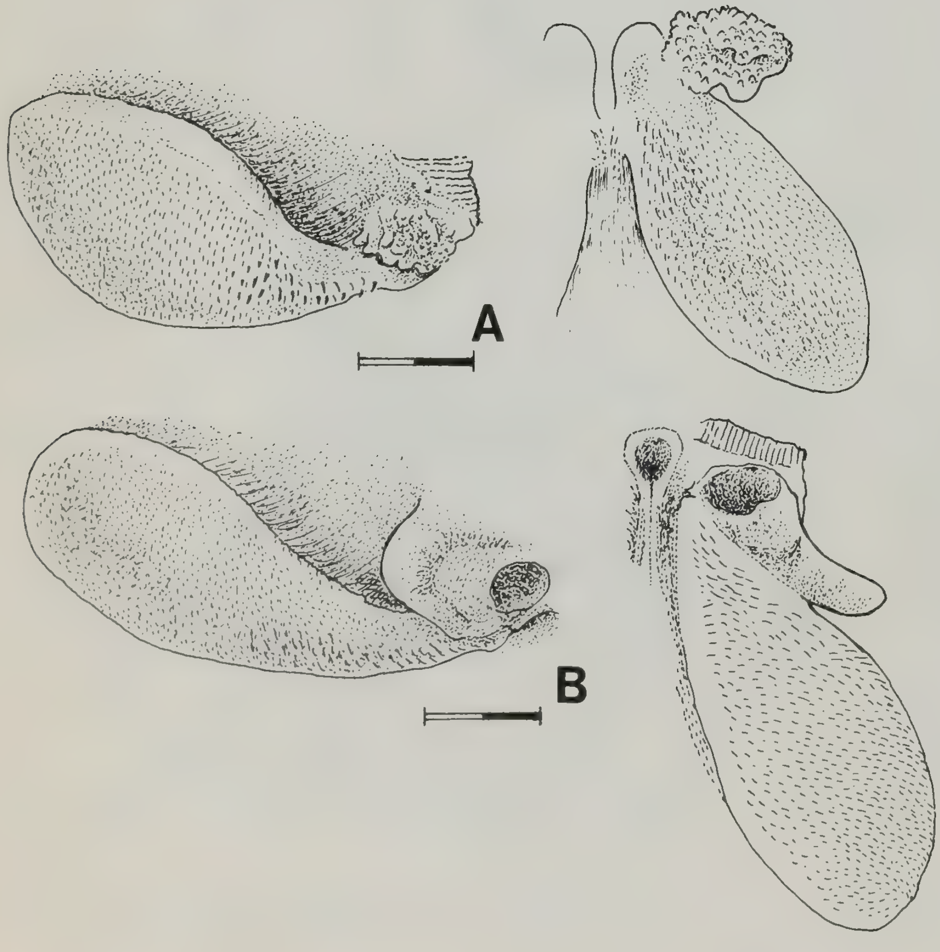

Fig. 13 PBO of A, *Myxus petardi* (BMNH 1914.8.20: 258–61, 118 mm SL); B, *Sicamugil hamiltoni* (1891.11.30: 80–81, 105 mm SL), in lateral and ventral views of right side.

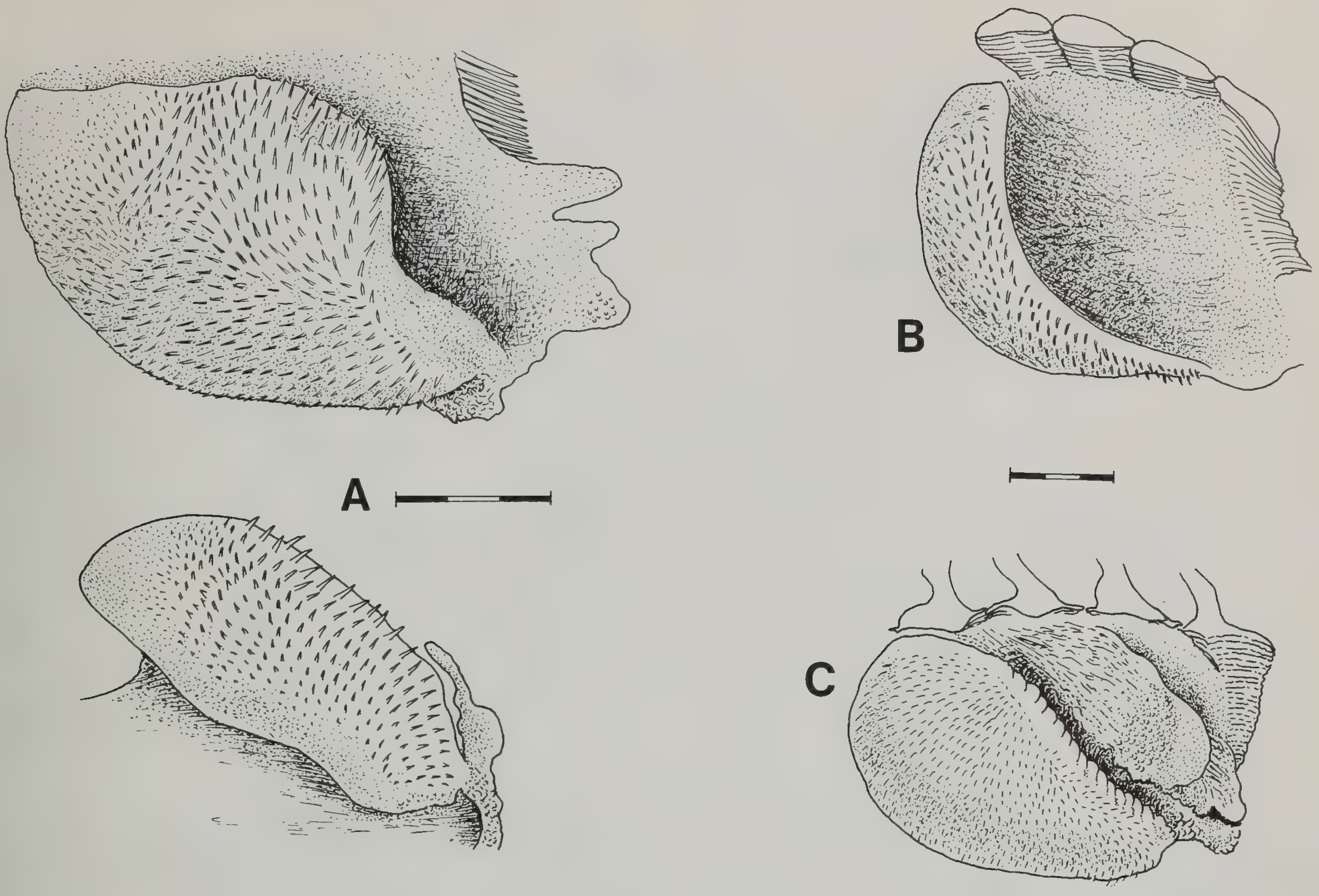

Fig. 14 PBO of A, *Neomyxus leuciscus* (BMNH 1877.7.24: 13, 200 mm SL), in lateral and ventral views (valve open forward); B, *Chaenomugil proboscideus* (1908.5.15: 278–9, 185 mm SL); C, *Chelon labrosus* (1962.7.30: 746, 107 mm SL). Lateral views of right side.

ventrally; sulcus diagonal and narrow, with a large fleshy, papillate valve and smaller ventral valve at lower end.

OEDALECHILUS Fowler, 1903 (Fig. 15): PBO with relatively small denticulate area, cushions widely separated, distal teeth evenly graded; sulcus diagonal, narrow, with fleshy valve and ventral finger-like process at lower end. This description applies to the type species, *O. labeo*, but in *O. labiosus*, the denticulate area is large, with abruptly graded distal-type teeth, those on the sulcus border being larger while those anterolaterally are posteriorly curved; sulcus border slightly concave, elevated dorsoposteriorly; sulcus nearly vertical, wide and with single large valve at lower end (Fig. 15B).

MUGIL Linnaeus, 1758 (Figs 16 & 17): In the type species, *Mugil cephalus*, from the Mediterranean, the PBO has a large denticulate area with finely size-graded teeth, those along the sulcus border being the largest; sulcus wide, near vertical, with a single large valve at lower end. In *M. cephalus* from other geographical areas there are marked differences in the sulcus and in valve size. Indeed, there seems as much intra- as interspecific variability in the organ, which casts doubt on the specific integrity of *M. cephalus*. Species with a PBO morphology similar to that in *M. cephalus s.s.* are *M. bananensis* (with finer teeth; Fig. 16F), *M. curema, M. trichodon* and *M. incilis* (Fig. 16G). In *M. capurii* the denticulate area is larger and bears longer, setiform teeth; the sulcus valve is triangular. *Mugil liza* has only a moderate denticulate area and a diagonal sulcus with small valve (*cf. M. cephalus* of Indian Ocean, Fig. 16A), features in which it more closely resembles some *Liza* species (see below). *Mugil hospes* has further differences; the denticulate area is extensive, being half the length of the entire PBO; the sulcus is nearly vertical, with a highly papillose valve (Fig. 17A). *Mugil thoburni* and *M. setosus* also differ from other *Mugil* in having a reduced denticulate area with greatly enlarged teeth along the sulcus border, and an extensive, vertical sulcus with a valve so large that it completely covers the sulcus' lower end (Fig. 17B).

CRENIMUGIL Schultz, 1946 (Fig. 15C): The description is of the condition in the type species, *C. crenilabis* (see below, p. 130). PBO with moderate denticulate area, teeth along sulcus margin setiform, in two rows; sulcus extensive, nearly vertical, its wall strongly papillate, especially that area overlying the central fat body; no valve at lower end, but a small fleshy nodule is present ventromedially.

LIZA Jordan & Swain, 1884 (Fig. 18): In one group of species the PBO has a moderately developed denticulate area with fine, almost evenly sized teeth; denticulate cushions deeply but narrowly separated; sulcus margin crenulated; sulcus diagonal and wide with two small valves (whose sizes are interspecifically variable) at lower end, the ventral one papillate. Species with this morphology are *L. aurata*, *L. buchanani*, *L. carinatus*, *L. curvidens*, *L. klunzingeri*, *L. macrolepis*, *L. saliens*, *L. ramada* (type species; Fig. 18A), *L. richardsonii*, *L. trichodon*. Species having a similar overall PBO morphology but lacking valves are *L. dumerilii*, *L. engeli*, *L. falcipinnis*, *L. haematocheilus*, *L. heterochilus*, *L. parvidens*, *L. parsia*, and *L. subviridis*. In *Liza haemato-*

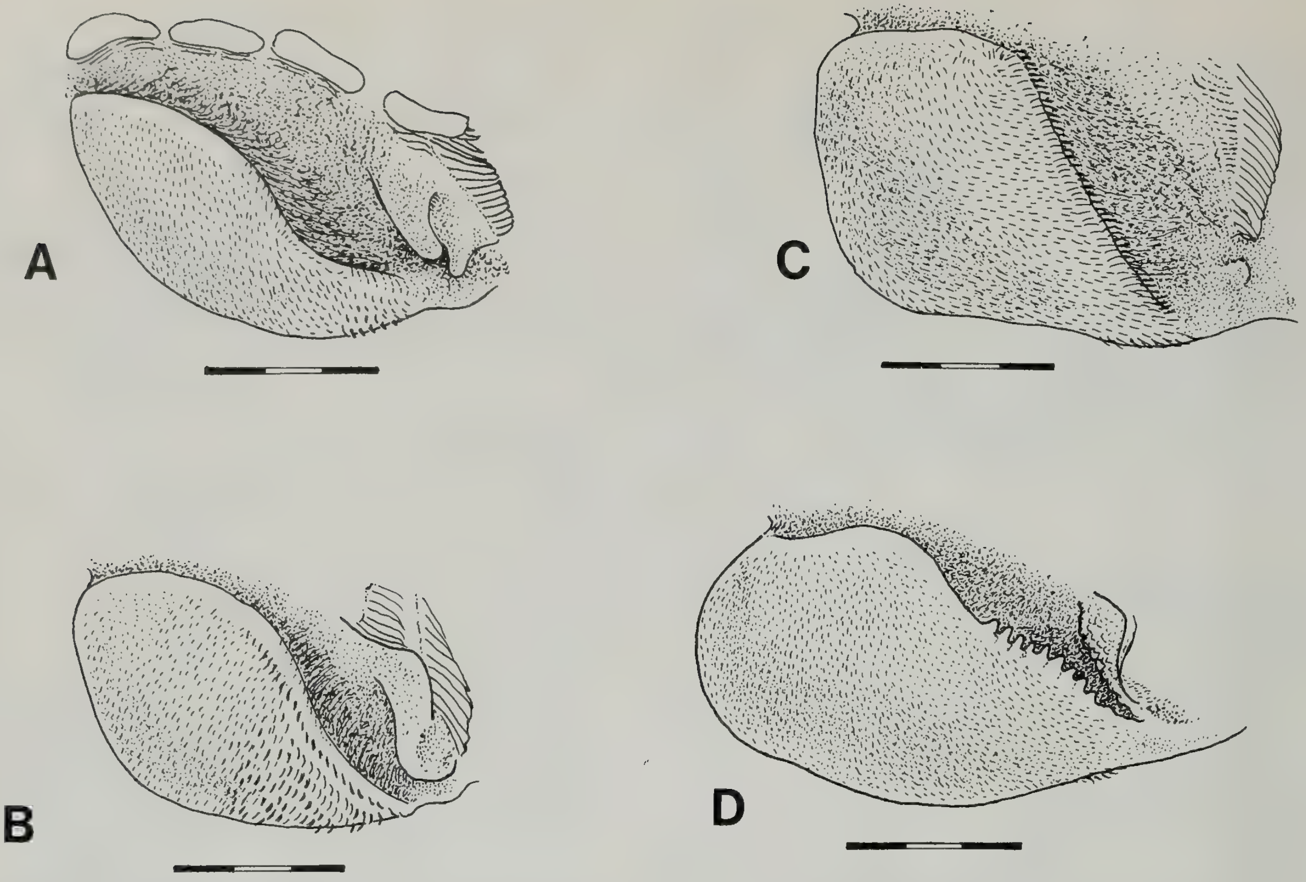

Fig. 15 PBO of A, *Oedalechilus labeo* (BMNH 1948.11.8: 1–10, 148.5 mm SL); B, *Oedalechilus labiosus* (1960.3.15: 1709–15, 83 mm SL); C, *Crenimugil crenilabis* (1951.11.16: 623–30, 107 mm SL); D, *Rhinomugil corsula* (1891.11.30: 89–98, 173.5 mm SL). Lateral views of right side.

cheilus, the sulcus is more extensive than in any other *Liza* and possibly mugilid species (Fig. 18B).

Liza abu more closely resembles *Mugil* in having both a large, lateral denticulate area and a large, single valve (Fig. 18E).

A third group of species with the denticulate area reduced, the teeth fine and evenly graded and the sulcus diagonal and wide, includes: *L. grandisquamis* (Fig. 18D), *L. parmatus*, *L. seheli* and *L. waigiensis* (Fig. 18C).

DISCUSSION

Agonostomus is the most plesiomorphic mugilid in terms of its PBO structure since it lacks the more developed organ of other taxa. The pharyngobranchial teeth are directly attached to the 2nd and 3rd pharyngobranchials and 4th toothplate; the *levator internus* 2 is narrow and the *retractor dorsalis* is a single (paired) muscle. These characters all seem to represent the least specialised condition seen in the Mugilidae. Schultz (1946) distinguished *Agonostomus* from other mugilids on the basis of what are plesiomorphic features *ie.*, broad band of teeth attached to jaw, lack of marginal teeth, absence of lip folds, broadly rounded lower jaw, long maxilla and absence of adipose eyefold tissue.

In constructing a phylogeny for the Mugilidae (Fig. 20) our polarity assignments for PBO morphotypes are based on the premises that *Agonostomus* represents the plesiomorphic lineage (on characters other than the absence of a PBO; see above) and that during ontogeny the more general precedes the less general condition (Løvtrup, 1978; Nelson, 1978; Fink, 1982). The latter sequence is evident in the possession of proximal-type pharyngobrancial teeth in the earliest stages of all mugilids which are later replaced by distal-type teeth in the majority of taxa (see 'Development'). Our hypothesis thus postulates that the more derived mugilid lineages are those in which distal-type teeth predominate. Those taxa which possess a greater variety of distal teeth morphotypes possibly represent advanced conditions, but more detailed investigations on dental variability are required to evaluate this suggestion.

Joturus is more advanced than *Agonostomus* in having a rudimentary sulcus between the pharyngobranchial toothplates, and in the development of a small, fat-body between epibranchials 2 and 3 (node 1 on Fig. 20); as in *Agonostomus*, there is a narrow *levator internus* and a single *retractor dorsalis*. *Cestraeus* also has a rudimentary sulcus with much-folded and papillose tissue covering a medial fat-body. Proximal-type teeth are present on pharyngobranchials 2 and 3 but the majority on the latter and those on toothplate 4 are of the distal-type. The *levator internus* 2 is somewhat larger than in the other two genera and the *retractor dorsalis* has some anterior fibres attached to the basioccipital (node 2 on Fig. 20). Schultz (1946) considered *Cestraeus* to be the most specialised of a group also including *Xenomugil*, *Chaenomugil* and *Neomyxus*, but there is no evidence from PBO morphology to support this relationship (see also p. 128). *Aldrichetta* has a PBO morphology 'intermediate' between those of the *Agonostomus—Cestraeus* series (Fig. 20) and those of other mugilids (see below). Like the *Agonostomus—Cestraeus* series, *Aldrichetta* exhibits some teeth on pharyngobranchial 3 which are of the proximal-type and there is a single *retractor dorsalis* although, as in *Cestraeus*, some anterior fibres attach to the basioccipital. In common with

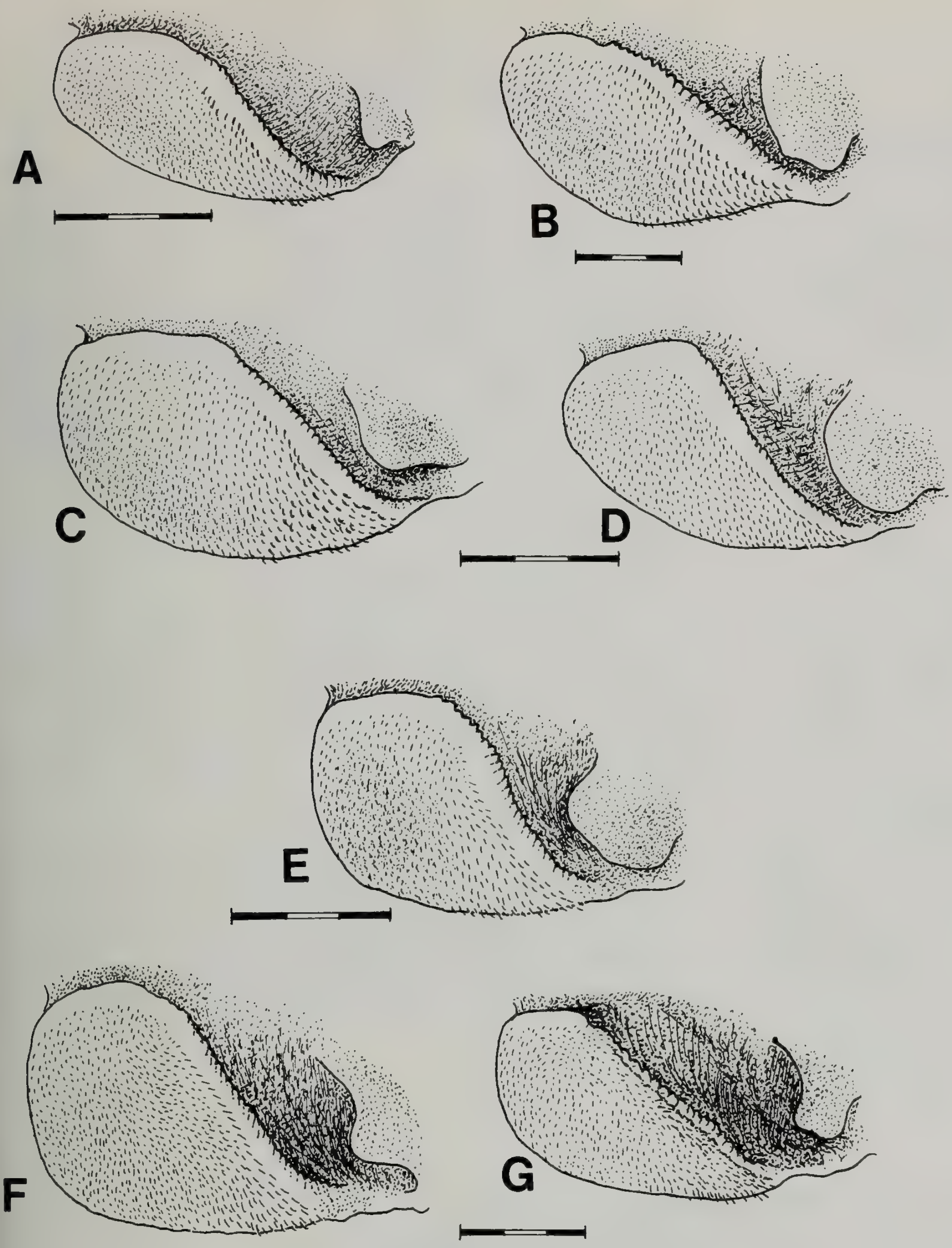

Fig. 16 PBO of *Mugil cephalus* from A, Socotra, Arabian Sea (BMNH 1957.4.24: 98–100, 81 mm SL); B, Kebir River, Latakia, Syria (1968.12.13: 462–4, 125 mm SL); C, Pacasmayo, Peru (1913.7.10: 41–4, 92.5 mm SL); D, Wakenoura, Japan (1923.2.26: 249–53, 73 mm SL); E, Kowie River, South Africa (1975.8.15: 204–212, 87.5 mm SL); F, *Mugil bananensis* (1968.11.15: 91–4, 120 mm SL); G, *M. incilis* (1933.8.2: 70–72, 117 mm SL). Lateral views of right side.

other mugilids there is a well-developed sulcus covering a medial fat-body (node 3 on Fig. 20), and a broad, thick *levator internus* 2.

There seems little doubt that on the basis of PBO morphology *Agonostomus*, *Joturus*, *Cestraeus* and *Aldrichetta* are distinct genera which represent successively advanced lineages (Fig. 20). *Aldrichetta* displays attributes of more advanced mugilids in its development of a sulcus and in having nearly all distal-type pharyngobranchial teeth. The presence of a fat-body and well-developed sulcus indicates a more advanced PBO.

The division of the *retractor dorsalis* into dorsal and ventral segments (dorsal and ventral referring to their insertions with respect to the *transversus* muscles rather than their origins which are both on the vertebral axis) together with the almost complete loss of fully mineralised and ankylosed (proximal-type) pharyngobranchial teeth and development of a sulcus and valves, characterises an advanced assemblage of mugilids which includes the more speciose genera. These genera constitute the two terminal subgroups of the cladogram (*ie.*, groups above nodes 4 and 5 on Fig. 20). It is these genera whose limits remain problematical. Schultz (1946) experienced 'great difficulty in arranging the species of Mugilidae into genera of concise and of clear definition, owing mostly to the paucity of useful taxonomic characters'. We believe that the PBO morphology is a character-complex that can aid in diagnosing groups.

Those genera which either lack a PBO or possess a rudimentary one *(Agonostomus*, *Cestraeus*, *Joturus*, *Aldrichetta*), have teeth on the 2nd pharyngobranchial and horizontally aligned 3rd and 4th pharyngobranchial toothplates, the condition which is present in early developmental stages of those taxa with a more advanced PBO. Thus, among the advanced assemblage of mugilids (*ie.*, those genera above node 4 on Fig. 20; see discussion above), an increased 4th toothplate area having its lateral surface more vertically orientated is taken to be a derived condition (node 5 on Fig. 20). Included in this group are *Myxus*, *Neomyxus*, *Chelon*, *Oedalechilus labiosus*, most *Mugil* spp, and *Xenomugil*. The plesiomorphic condition, where the 4th toothplate lies nearly horizontally exposing a relatively small, convex lateral denticulate area, is present in *Sicamugil*, *Rhinomugil*, *Chaenomugil*, *Oedalechilus labeo*, *Crenimugil*, and most *Liza* spp. The size of the denticulate area is often negatively correlated with that of the sulcus, since generally the more extensive the

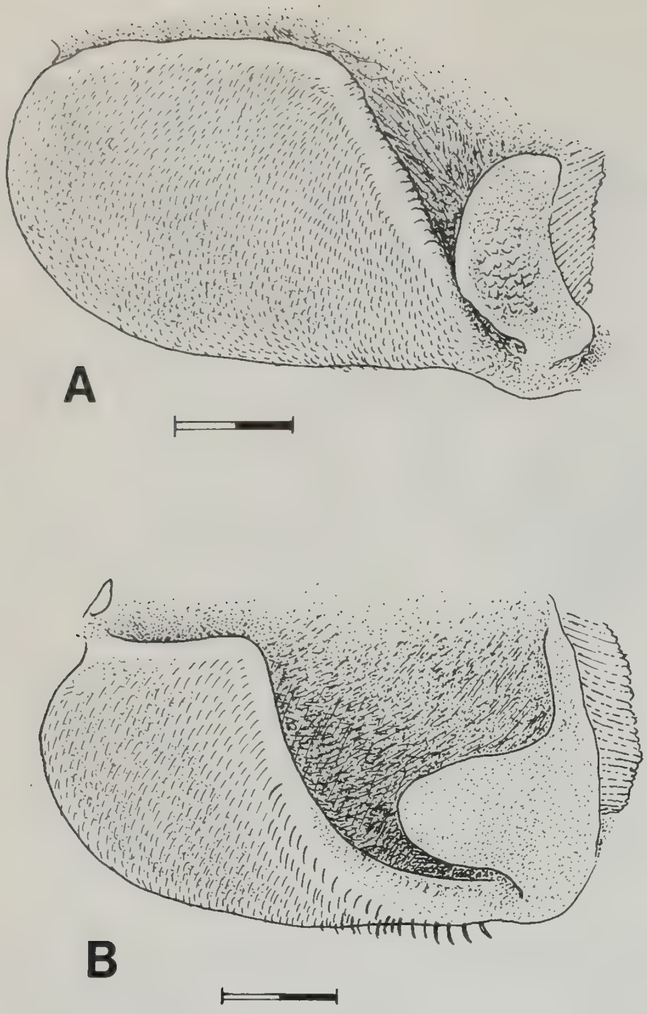

Fig. 17 PBO of A, *Mugil hospes* (BMNH 1975.10.7: 1–2, 156.5 mm SL); B, *M. thoburni* (1901.6.26: 170–1, 153 mm SL). Lateral views of right side.

former, the narrower the latter (*eg.*, *Mugil hospes*, *Neomyxus leuciscus*). An extensive sulcus may not, however, indicate the plesiomorphic state since in those taxa with wide sulci (eg. *Liza haematocheilus*) the length of the entire PBO is increased due to the increased distance between the 2nd and 3rd epibranchials.

Considering first the genera exhibiting the more derived condition (*ie.*, those above node 5 on Fig. 20), *Myxus* has a PBO morphology similar to that of some *Mugil* species, but differs from these and other mugilids in its convex denticulate sulcus border. We follow Ingham (1952) in including *Trachystoma petardi* in the genus since its PBO morphotype and jaw dentition are nearly identical to those of the type species *M. elongatus*. Schultz (1946) included in *Trachystoma*, *Mugil capensis* Cuv. & Val., 1836 (= *M. euronotus* A. Smith, as given in Schultz). However, *Mugil capensis* is unlike the other two species in both the form of its PBO and its jaws, the former resembling more closely that of *Mugil cephalus*, the latter those of *Mugil curvidens*.

Neomyxus shares PBO characters (extensive denticulate area, vertical and narrow sulcus) with *Mugil hospes*. Thought by Schultz (1946) and Ingham (1952) to be closely related to *Chaenomugil*, it differs considerably from this taxon in PBO morphology (see p. 124) and lower jaw shape. Although the lower lip of *Chaenomugil* is dependent as in *Neomyxus*, the labial teeth are bicuspid, short, and somewhat posteriorly directed.

Chelon has a similar PBO morphology to some *Liza* species in possessing two valves, but the upper of these is highly papillose (*cf.* the lower in *Liza*). Schultz (1946) unjustifiably synonymised *Liza* and *Oedalechilus* with *Chelon*; *Oedalechilus*, as represented by the type species *Mugil labeo* Cuvier, was thought by Schultz to represent 'the most extreme development of the mouth of *Chelon*'. Trewavas & Ingham (1972)

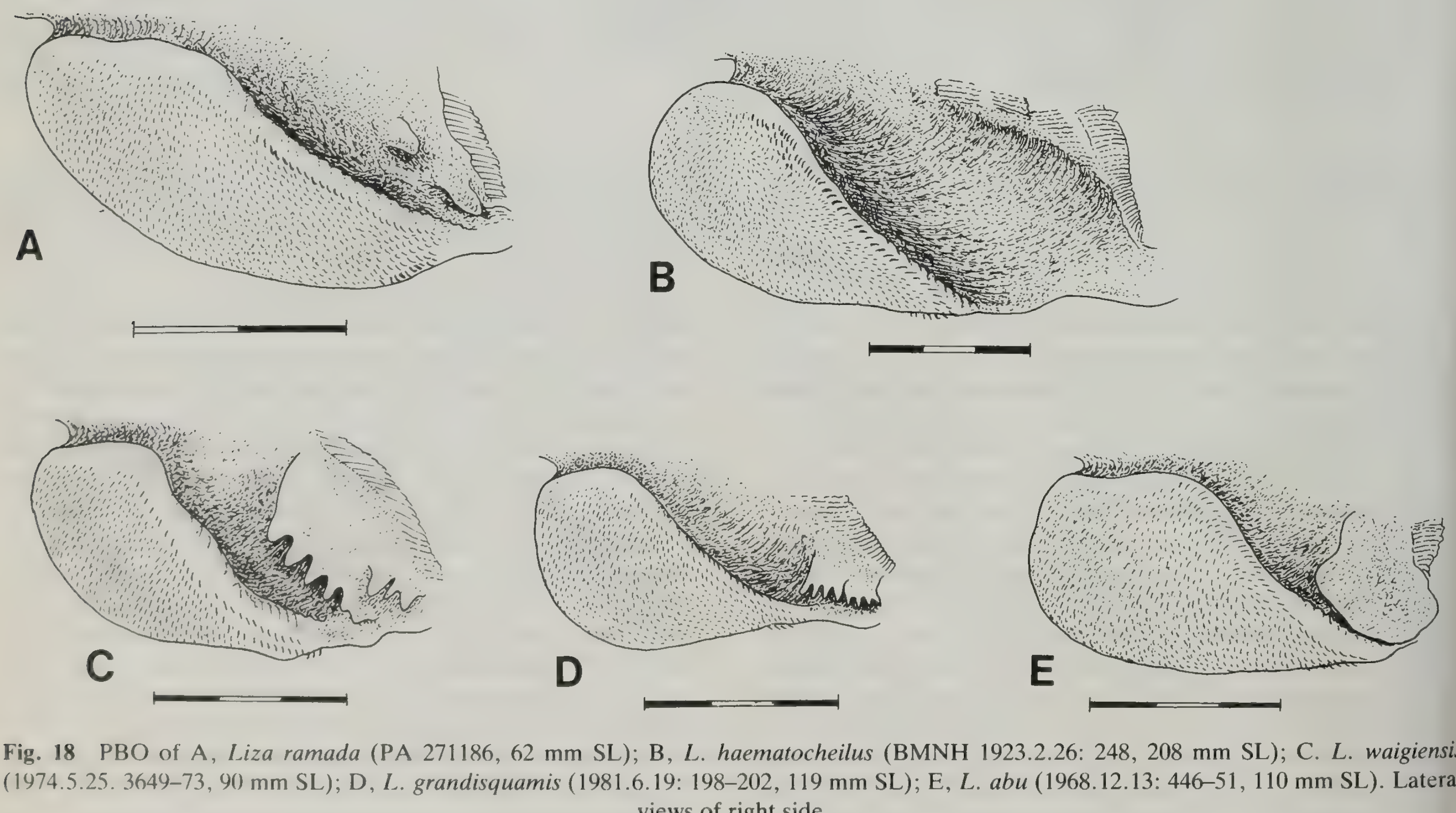

Fig. 18 PBO of A, *Liza ramada* (PA 271186, 62 mm SL); B, *L. haematocheilus* (BMNH 1923.2.26: 248, 208 mm SL); C. *L. waigiensis* (1974.5.25. 3649–73, 90 mm SL); D, *L. grandisquamis* (1981.6.19: 198–202, 119 mm SL); E, *L. abu* (1968.12.13: 446–51, 110 mm SL). Lateral views of right side.

regarded *Mugil labiosus* Val. as a species of *Oedalechilus* which Schultz (1953) had made the type species of *Plicomugil*. There are, however, distinct differences in the PBO's, and in the nature of the lip folding, tooth shape and lower jaw shape between *O. labeo* and *O. labiosus* (p. 125). We thus accept *Plicomugil* as a valid genus to contain *O. labiosus* which exhibits the expanded denticulate area typical of the derived condition (node 5 on Fig. 20), (*cf. O. labeo*).

Mugil has a variable PBO morphology and among the species examined, five groups can be distinguished (see p. 125 for description of the features delimiting these groups), *viz*: 1) including *M. cephalus* (type species), *bananensis*, *curema*, *curvidens*, *incilis* and *trichodon*; 2) *M. capurii*, considered by Ingham (1952) the most primitive *Mugil* species (certainly the wide and shallow separation of the denticulate cushions and large proximal teeth are plesiomorphic features); 3) *M. liza* which more closely resembles *Liza* species; 4) *M. thoburni* and *M. setosus*, which are certainly closely related species and may represent the respective ends of a clinal distribution, the former in the Galapagos, the latter at the western coast of Mexico (Schultz (1946) recognised *Xenomugil* to contain *M. thorburni*); 5) *M. hospes*, which in the feature of its vertical sulcus most closely resembles *Neomyxus leuciscus*, but the overall PBO morphology and valve size suggests that it is a specialised variant of the *M. cephalus* group.

Now considering the advanced genera which exhibit the more plesiomorphic condition of a relatively small denticulate area (*ie.*, terminal group of Fig. 20), *Sicamugil* has a *Liza*-like PBO morphology although with specialised features (p. 124). Schultz (1946) synonymised *Sicamugil* with *Trachystoma* (=

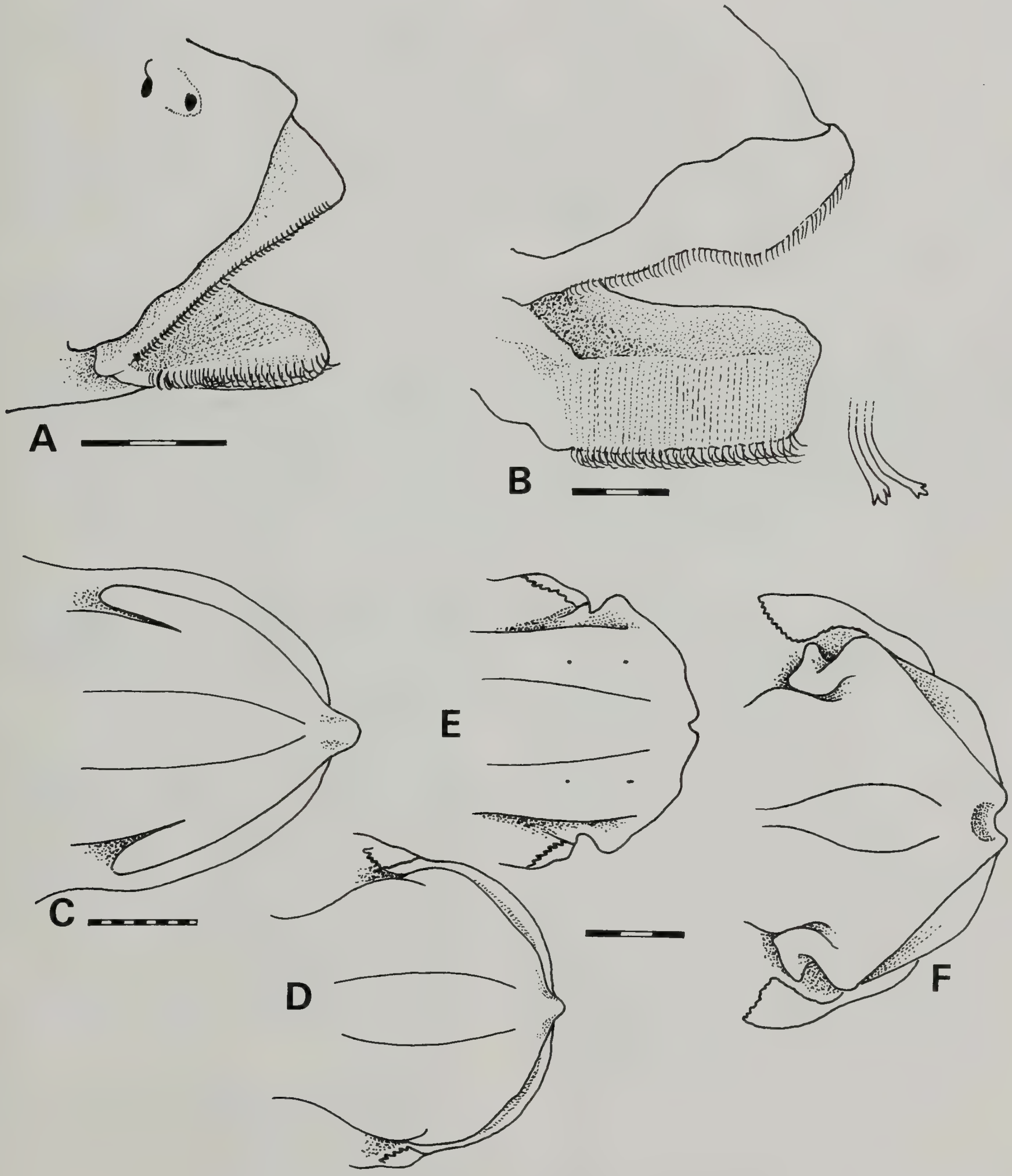

Fig. 19 Jaw dentition (lateral views) in A, *Chaenomugil proboscideus* (BMNH 1908.5.15: 178–9, 185 mm SL); B, *Neomyxus leuciscus* (1877.7.24: 13, 200 mm SL), the tips of the teeth are shown enlarged. Lower jaw shape (ventral views) of C, *Mugil capurii* (1933.2.28: 1–2); D, *Mugil curema* (1891.5.12: 33–42); E, *Liza abu* (1986.1.31: 1–3); F, *Liza waigiensis* 1974.5.25: 3649–73), a shape associated with a specialised PBO valve-type (see text).

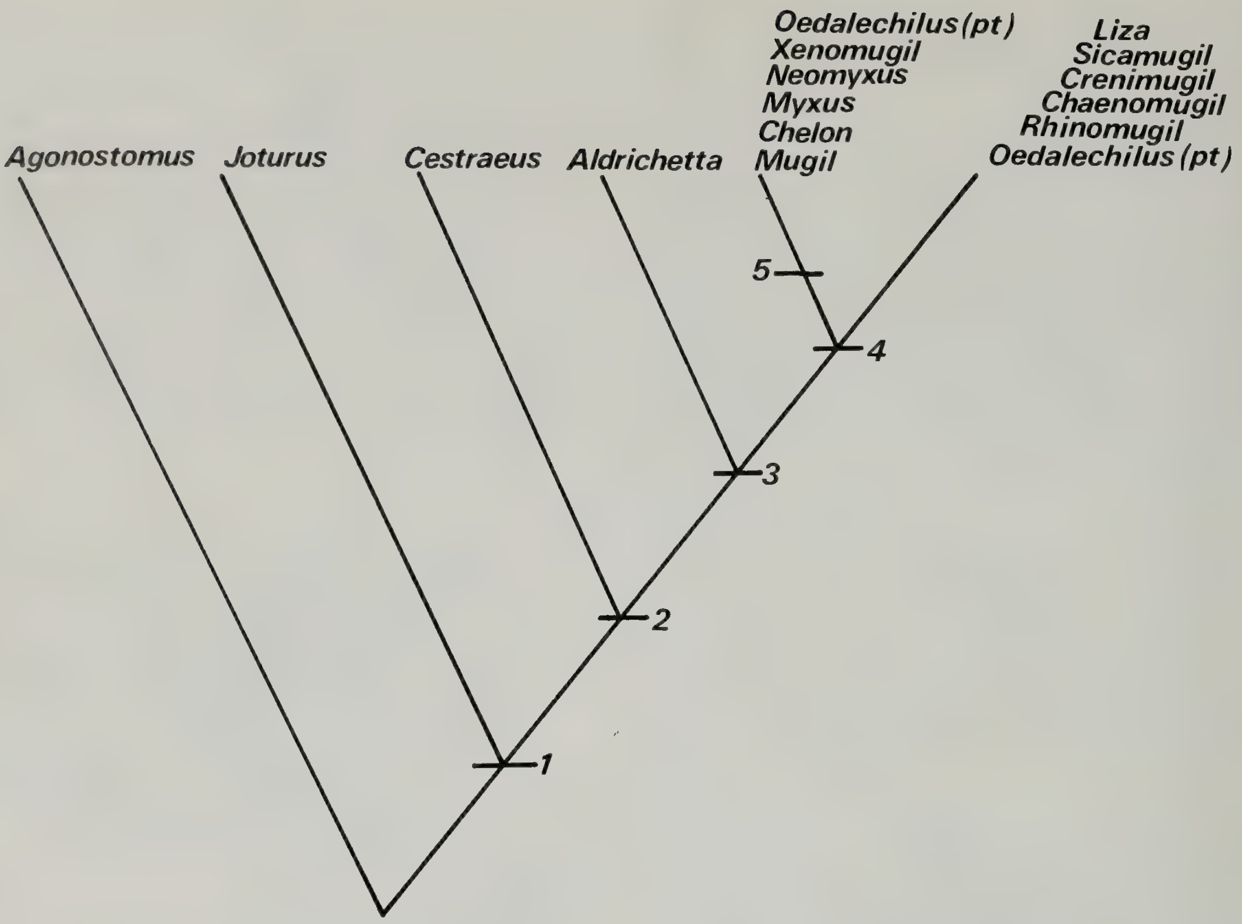

Fig. 20 Cladogram of mugilid genera based on pharyngobranchial organ synapomorphies, *viz*. 1) Development of rudimentary sulcus and fat body. 2) Majority of pharyngobranchial teeth are distal-type; partial attachment of *retractor dorsalis* muscle to basioccipital. 3) Sulcus and anterior fat-body well-developed; all teeth, apart from those on anteromedial area of 3rd toothplate are distal-type. 4) PBO completely developed with anterior and posterior fat-bodies, well-formed sulcus, enlarged, modified pharyngobranchial toothplates, teeth lost from pharyngobranchial 2; *retractor dorsalis* distinctly divided anteriorly into dorsal and ventral segments, the dorsal originating from the basioccipital. 5) Toothplates with outer margins vertically aligned; sulcus deep and narrow. Although several PBO apomorphies characterise taxa of these two lineages, none appear to be synapomorphic (see text).

Myxus; see above), but in lower jaw morphology *Sicamugil* appears to belong with those *Liza* species having a moderately developed denticulate area (see above).

Rhinomugil has a PBO morphology resembling that of *Liza*, in both the area and shape of its sulcus. Like many *Liza* it has an acute ventral profile to the lower jaw and differs only in its longer snout and wide separation of anterior and posterior nasal openings. *Squalomugil* Ogilby (type species *Mugil nasutus* De Vis) is a synonym (see Schultz, 1946).

Chaenomugil has a reduced denticulate area and extensive sulcus, features shared with a group of *Liza* species (p. 126). *Crenimugil* has PBO features and an angular lower jaw shape characteristic of *Liza*. Trewavas & Ingham (1972: 21) considered *Mugil heterochilus* and *M. macrochilus* to belong to the same 'evolutionary series' as *Crenimugil crenilabis* thus implying their inclusion in that genus. We find, however, that the PBO of *Mugil heterocheilus* more closely resembles that of *Liza* spp and refer it to that genus (p. 125). We have not seen a specimen of *M. macrocheilus*.

Liza species fall into three groups on PBO morphology; (1) the more speciose, exemplified by *L. ramada* (see p. 125 for other species, and characters delimiting this group), (2) differing from the first group in lacking valves, exemplified by *L. falcipinnis*, and possibly *L. haematocheilus* which also lacks valves but has a more extensive sulcus (p. 125), (3) characterised by a more reduced denticulate area and wide sulcus. This latter group has a marked angular lower jaw shape (Fig. 19F). *Mugil liza* has a PBO morphotype typical of the *Liza ramada* group, except in having a single rather than a double valve in which respect it closely resembles *Liza abu* (p. 126).

The morphotype groupings of the PBO support, to a large extent, the present recognition of mugilid genera but at the same time indicate that the speciose genera *Liza* and *Mugil* are possibly non-monophyletic assemblages. Certainly there are species-specific PBO morphotypes (see above for examples in *Mugil* and *Liza*). Sulcus valve morphology is distinctive enough to categorise some groups of taxa (*eg*., the crenulate type restricted to some *Liza* species; p. 125). We argue that these represent derived groupings since ontogenetically, valves originate from a double pharyngobranchial tissue fold similar to that present in adult *Joturus* (p. 124) which covers the area between the 2nd and 3rd pharyngobranchials. Absence of valves is also taken as a derived (loss) condition.

The distribution of the homologues discussed above and the groupings summarised in the cladogram (Fig. 20) might serve as a basis for re-diagnosing genera. Jordan & Evermann (1896) recognised *Agonostomus* as belonging to a separate subfamily and in a formal classification of our phylogenetic hypothesis this would be so. We recognise it as being the plesiomorphic lineage of other mugilids (p. 126). That the Mugilidae is, itself, a monophyletic group is amply borne out by the derived nature of the upper gill-arch elements and their associated musculature; shared derived features of the lower gill-arch musculature indicate a sister-group relationship with atherinomorphs (Stiassny, 1990). Stiassny (1991) has also suggested an alternative relationship with 'higher percomorphs'.

In microphagous euteleosts a filtering pharyngeal organ is always developed from modifications to the epibranchials, noticeably involving hyperdevelopment of the 4th. Nelson (1967) reviewed the structure of the epibranchial organ among these fishes and concluded that such structures had not evolved in higher teleosts because an advanced structural organisation involving the *retractor dorsalis* muscle precludes such development. Nelson noted that the *retractor dorsalis* confers a manipulative role to the upper pharyngeals (pharyngobranchials) and that any specialisations of the upper gill-arches in higher teleosts involve the pharyngobranchials. The structural modifications to the upper gill-arches in Mugilidae have involved the unity and expansion of the 3rd pharyngobranchial and the 4th toothplate, and their manipulation has been refined by the division of the *retractor dorsalis* and the hypertrophy and forward shift of the 2nd *levator internus*. Unlike the euteleostean epibranchial organ, which is essentially an 'internal' structure whereby the posterior gill-arches are enclosed within a diverticulum, in mugilids the pharyngobranchial organ is an external structure with the gill-arches surrounding it.

A close parallel occurs between mugilids and the cyprinid *Hypophthalmichthys* in which the gill-arches surround the main body of the epibranchial organ which is manipulated by a forwardly directed and divided *adductor hyomandibularis* muscle (the functional homolgue of the 2nd *levator internus* of mugilids). *Hypophthalmichthys* differs from mugilids in having the epibranchials enclosed in internal ducts within the epibranchial organ, such that detrital material is filtered first externally and then passes into the organ for further processing (Howes, 1981). Mugilids, presumably because of the 'restriction' imposed by the *retractor dorsalis*, have not evolved an invaginated organ but have utilised that muscle to permit a degree of manipulation resulting in a highly selective trophic apparatus not available to the cyprinid.

Fine particulate matter is a richer source of adsorbed and absorbed nutrients than coarser material (Wood, 1964; Odum, 1968) and the majority of mugilids utilise such a resource with, perhaps, a capacity to be selective in the process (see functional discussion above). In so doing, mugilids exploit a resource unavailable to most other fishes and are largely freed from any competitive interaction, thereby permitting them to occupy habitats denied to other taxa (Hartley, 1940; Hickling, 1970; Odum, 1970; Capanna *et al.*, 1974). Moreover, mugilids being the fundamental harvesters in those communities, provide the agency for converting a low-grade unavailable resource into a high-grade available one (Hiatt, 1944; Odum, 1970; Brusle, 1981).

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Cranial anatomy and phylogeny of the South-East Asian catfish genus *Belodontichthys*

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SYNOPSIS. The cranial anatomy of the south east Asian silurid catfish *Belodontichthys dinema* (Bleeker, 1851) is described. Comparison is made with other members of the Siluridae and a suite of synapomorphies identified. From these it is inferred that *Belodontichthys* is the sister-group to *Ompok bimaculatus* and they, in turn, form the sister-group to *Wallago*. The genera '*Ompok*' and '*Kryptopterus*' are recognised as non-monophyletic assemblages. Neurocranial features of *Belodontichthys* are examined in the context of their function and hypothesised evolutionary development.

INTRODUCTION

The genus *Belodontichthys* was proposed by Bleeker (1858) in his revision of siluroid fishes. The genus consisted of the type species (*dinema*) which he had previously described as a member of the genus *Wallago* (Bleeker, 1851). Bleeker's specimens were from Borneo; since then the species has been recorded from Sumatra, Java, Laos, Vietnam, Thailand, Kampuchea and Malaysia (Haig, 1950; Kottelat, 1985, 1989; Roberts, 1989). The genus is currently recognised as monotypic and assigned to the family Siluridae.

Even for a siluroid *Belodontichthys* has an extraordinary external morphology (Fig. 1A). The fish is elongate, strongly compressed with a long anal fin (85–97 rays), short dorsal fin (4 or 5 rays) and a small but deeply forked caudal fin. The pelvin fins (9 or 10 rays) are minute but the pectoral fin (18–21 rays) is elongate and wing-like, extending to beyond the anal fin origin. The head is narrow with a straight to concave dorsal profile (formed by the anteriorly extended dorsal body musculature) (Fig. 1B). The eyes are large, set at the corner of the mouth; the jaws long, and obliquely angled, with the lower jaw extending anteriorly beyond the upper (Figs 1B, C); both jaws are armed with three rows of long teeth with arrow-shaped tips. The maxillary barbel extends only to the pelvic fins; and the single pair of mandibular barbels are shorter than the diameter of the eye. Gill-rakers are elongate, numbering *ca* 30.

In spite of its peculiar morphology, the anatomy of *Belodontichthys* has not previously been described. Perhaps this is because it is not abundant in museum collections although relatively common in nature (Haig, 1950). This paper is the result of the collection by one of us (A.F.) of specimens in Thailand which has provided the opportunity for a detailed anatomical investigation. Our study is restricted to the anatomy of the neurocranium, jaws, hyomandibular and palatoquadrate osteology and associated myology. It is hoped, however, that future work by one of us (A.F.) will describe the other skeletal structures. Despite the anatomical limitation of our investigation we believe it has uncovered several previously unknown features which point the way to a more refined phylogenetic analysis of the Siluridae.

The habits of *Belodontichthys* are poorly known. Smith (1945) remarks that the fish occurs in deeper waters and feeds on migratory schools of young cyprinids. We are informed by Mr Chavalit Vidthayanon that the fish usually stays close to the substrate or in the middle of the water column but takes its prey from near the surface. Adults congregate in small groups of 5–10, subadult groupings usually comprise more than 10 individuals. Adults feed primarily on fishes, and juveniles on insects and crustaceans. Eggs are adhesive.

The pelagic and predatory habits of *Belodontichthys* apparently resemble closely those of the schilbeid siluroid *Europiichthys vacha* which according to various accounts

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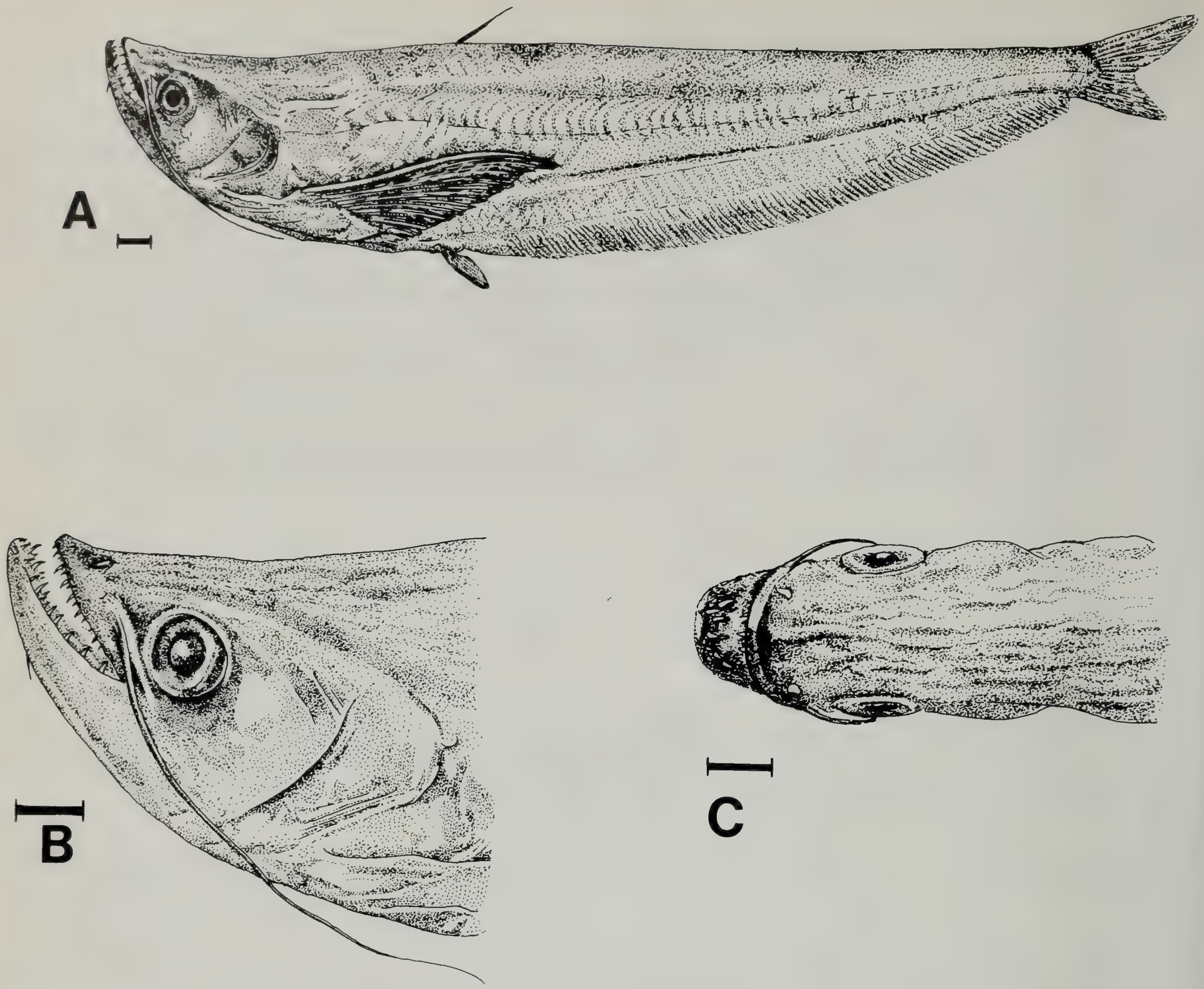

Fig. 1 *Belodontichthys dinema*: A, lateral view of the whole fish; B, lateral view of head; C, dorsal view of head showing overlap of teeth in the upper jaw by those in the lower jaw. Drawn from LILI 89007, 320mm SL. Scale bars = 10mm.

reported by Hora (1937) is also a fast-moving pelagic and voracious fish (see p. 158).

METHODS AND MATERIALS

In making our phylogenetic analysis we have concentrated principally on in-group comparisons to other silurids since our concern has been the immediate relationships of *Belodontichthys*. The monophyly of the family Siluridae has been demonstrated by Bornbusch (1988; 1990) and corroborated by our out-group comparisons with a wide-range of siluroid taxa involving the families Ariidae, Bagridae, Clariidae, Diplomystidae, Ictaluridae, Pangasiidae, Pimelodidae, Plotosidae Schilbeidae and Sisoridae. In making out-group comparisons we have accepted that the Diplomystidae represent the sister-group to all other siluroids and so follow Grande (1987) in recognising a primary division of the Siluriformes into the Diplomystoidei plus Siluroidei.

Although we have also used Grande's (1987) description of the Eocene †Hypsidoridae as a source for comparisons we are less sure that it truly represents the sister-group of all other siluroid families as proposed by Grande since †*Hypsidoris* seems to possess several advanced features shared with some siluroids (T.P. Mo pers. comm.).

Nomenclature: Osteological nomenclature follows that of Patterson (1975). We have adopted the term posttemporosupracleithrum used by Arratia (1987) since we believe this most satisfactorily describes the structure whose incorporated elements are a matter of debate (Lundberg, 1975; Fink & Fink, 1981; Howes, 1983*a*; Arratia, 1987). Muscle nomenclature follows that of Winterbottom (1974). Reference to *Ompok* in comparative sections refers to *O. bimaculatus* (particularly specimens from the Sittang River, Myanmar); see p. 155 for further discussion.

List of specimens used for anatomical study: (BMNH = Collections of the Natural History Museum, London; IBRP = Research Institute of Evolutionary Biology, Tokyo University of Agriculture; LILI = Ligong Laboratory of Ichthyology, Tokyo; ZMA = Institute of Taxonomic Zoology, University of Amsterdam). Preparations; CS = cleared and stained; D = dissected; S = dry skeleton):

Aorichthys aor BMNH 1891.11.30:224, Sittang R. Myanmar (S, cranium 65 mm); *Bagarius yarrelli* 1889.8.29:2, Hooghly R., India (S, cranium, 515 mm); *Bagrichthys macracanthus* BMNH Uncat. locality unknown (D, 110 mm SL); *Bagrus bayad* BMNH Uncat., Nile (S, cranium 118 mm); *Belodontichthys dinema* LILI 89008 (D, 343 mm SL, cranium 51.5mm); LILI 89002 (CS, 150 mm SL); LILI 89007 (D, 320 mm SL); LILI 89002 (D, 125.5 mm SL) all Ubonratchauthani, Thailand; IBRP 6625 Singtang market, West Kalimantan, Indonesia. (D, 202mm SL, cranium, 34.5mm); *Chrysichthys cranchii* BMNH 1900.12 Albertville, Tanganyika (S, cranium 118mm); *Eutropiichthys vacha* BMNH 1891.11.30:162–9 (D, 175mm SL), (S, cranium 39mm) both, Sittang river, Myanmar; *Hemisilurus heterorynchus* BMNH 1982.3.29:161–2 Kapuas, Borneo, Indonesia (D, 250mm SL, S, cranium 41.5mm); *Hito taytayensis* 1933.3.11:110–2 Culion, Philippines (D, 148mm SL); *Ictalurus punctatus* 1898.12.29:171 Arkansas (S, cranium 33.5mm); *Kryptopterus amboinensis* 1864.5.15:4 No locality (D, 128mm SL); *K. apogon* LILI 89016 (D, 195mm SL; S, cranium 74mm); LILI 89010 (D, 123mm SL; S, cranium 31mm) both from Moon R., at Khong Chiam, Ubonratchathani, Thailand; *K. bleekeri* LILI 89030 Borapet canal at Bung Borapet Fisheries Station, Nakorn Sawan, Thailand (D, 194mm; 250mm SL; S, cranium 34mm from 149mm SL specimen); *K. bicirrhis* BMNH 1982.3.29:163–7 Kapuas R., Borneo (CS, 58mm SL; D, 60mm SL); *K. cryptopterus* LILI 89009 Borapet Canal (CS, 102mm SL; D, 105, 115 mm SL); BMNH 1982.3.2.168 Kapuas R. (D, 112 mm SL); *K. limpok* BMNH 1980.12.16:18 Vientiane (D, 230 mm SL); 1891.1.27:14 (S, cranium 26 mm); *K. cf. macrophthalmus* BMNH 1905.1.26:5 Borneo (D, 221 mm SL); *K. micronema* BMNH 1892.9.2:25 Simbang R., Borneo (D, 280mm SL); *K. moorei* LILI 89018 Moon R., Haad Saeng Thian, Thailand (D, 155mm SL; D, 161mm SL, and cranium, 24mm); *Mystus nemurus* Lake Bung Borapet, Nakorn Sauan, Thailand (S, cranium 24mm); *Ompok bimaculatus* LILI 85003 (D, 137mm SL), BMNH 1889.2.1:2477–8 (D, 170; cranium, 31.5mm), 1891.11.30:179 (S, cranium 35.5mm) both Sittang R., Burma, 1889.2.1:2499–504 Sind (D, 110mm SL, cranium 18mm); *O. liacanthus* BMNH 1891.1.27:15–27. Kapuas (D, 112mm SL); *O. pabo* BMNH 1891.11.30:180–3 Sittang R. (D, 202mm SL); *Pteropangasius cultratus* LILI 89035 Nakorn Sawan, Thailand (S, cranium 39mm); *Pimelodus maculatus* BMNH 1861.1.19:24 Sao Paulo (S, cranium 49mm); *Plotosus caneus* 1889.2.1:2529 Calcutta (S, cranium 60mm); *Proeutropiichthys taakree* 1891.11.30:199 Sittang (S, cranium 60mm); *Schilbe mystus* 1982.4.13:3242–50 Nigeria (D, 106, 107mm SL); *S. uranoscopus* 1850.7.29 Nile (S, cranium 58mm); *Silurichthys hasseltii* 1970.9.3:178–82 Singapore (D, 83mm SL); *Silurus asotus* BMNH Uncat. (cranium 65mm); 1983.7.6:13–19 Fukien (CS, 65mm SL); *S. glanis* BMNH Uncat. (S, crania, 105, 114mm), 148a (S, cranium 62mm); *S. triostegus* 1969.3.3:168–76 (Basrah (CS, 105mm SL; D, 215mm SL); *Wallago attu* BMNH Uncat. (S, cranium 98mm), 1891.11.30:156–161 Sittang R., (D, 350mm SL), Uncat. (S, cranium 84mm); LILI 89074 Weekend Market, Bangkok, Thailand (CS, 100mm SL); *W. leeri* BMNH 1880.4.21:203 No locality (D, 275mm SL, cranium extracted 57mm).

Other specimens examined: *Belodontichthys dinema* (syntype of *B. macrochir*) BMNH 1863.12.4:64 Borneo (266 mm SL); ZMA 120.684 Sumatra (195, 210, 235, 245 mm SL); *Kryptopterus schilbeides* BMNH 1892.3.29:173 Kapuas (80 mm SL); *Ompok bimaculatus* ZMA 120.549 Orissa (145 mm SL), BMNH 1980.12.16:19 Vientiane (155 mm SL); *O. eugeneiatus* BMNH 1982.3.20:174 Kapuas (91 mm SL); *O. pabda* ZMA 15.541 Pakistan (91 mm SL).

Abbreviations used in figures

A1, A2,	outer and inner divisions of *adductor mandibulae* muscle
aa	anguloarticular
AAP	*adductor arcus palatini* muscle
af	anterior fontanelle
afc	anterior branch of frontal canal
AH	*adductor hyomandibularis* muscle
afo	opening of anterior frontal canal
amf	adductor mandibulae fossa in pterotic
AO	*adductor operculi* muscle
apm	ascending process of premaxilla
apt	anterior pterygoid
AW	mandibular division of *adductor mandibulae* muscle
bo	basioccipital
bof	basioccipital facet
br	buccal ramus of trigeminal nerve
cco	cross-commissure opening
cl	cleithrum
cm	coronomeckelian bone
de	dentary
DO	*dilatator operculi* muscle
epo	epioccipital
EPX	epaxial muscle
ET	*extensor tentaculi* muscle
exo	exoccipital
fc	frontal crest
fco	opening of lateral branch of frontal canal
ff	facial nerve foramen
fg	glossopharyngeal foramen
fh	foramen for hyomandibular trunk of facial nerve
fhy	foramen for hyoid nerve
fim	foramen for internal branch of hyomandibular nerve
fm	foramen magnum
fo	foramen for optic nerve
fr	frontal
ft	foramen for trigeminal nerve
ftf	foramen for trigeminofacialis trunk
fv	foramen for vagus nerve
hy	hyomandibular
hyf	hyomandibular fossa
IM	*intermandibularis* muscle
io	infraorbital
lac	LAP crest on hyomandibular
LAP	*levator arcus palatini* muscle
le	lateral ethmoid
lea	lateral ethmoid articular facet
lfc	lateral branch of frontal canal
LO	*levator operculi* muscle
me	mesethmoid
mec	mesethmoid cornu
mo	mandibular canal opening
mx	maxilla

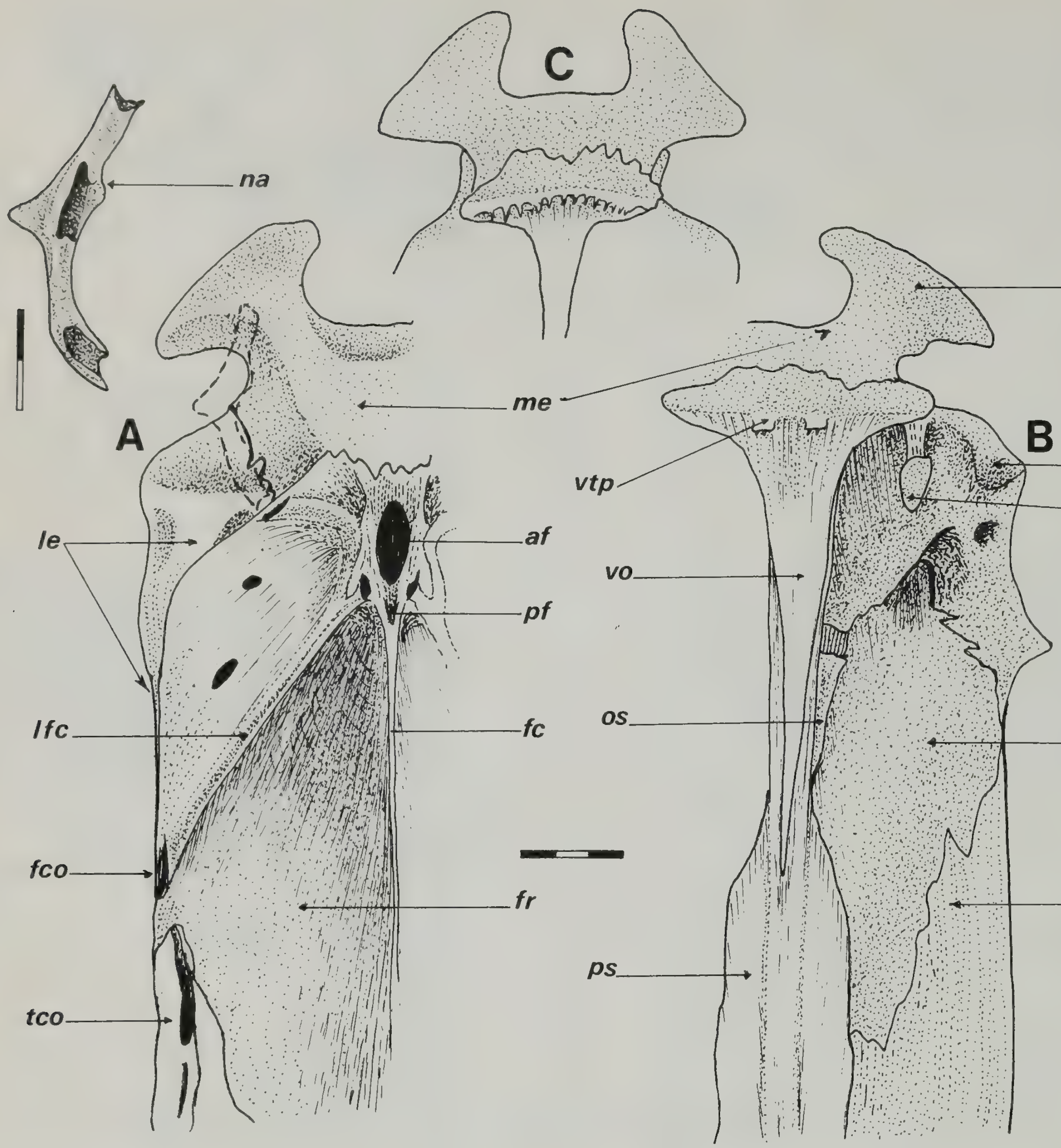

Fig. 2 *Belodontichthys dinema*: anterior part of neurocranium in A, dorsal and B, ventral views (51.5mm cranium, LILI 89008); C, ventral view of Indonesian specimen (34.5mm cranium IBRP 6625) showing difference in vomerine tooth pattern. In A, the nasal bone is shown shifted laterally and slightly enlarged; its position *in situ* is indicated by a dashed outline on the main figure. Scale bars on this and succeeding figures are in mm divisions.

na	nasal
no	optic nerve
os	orbitosphenoid
pal	palatine
pf	posterior fontanelle
pmx	premaxilla
po	preoperculum
ppt	posterior pterygoid
pro	prootic
prs	prootic spur
ps	parasphenoid
psc	posttemporosupracleithrum
psk	parasphenoid keel
pss	parasphenoid shelf
ptc	pterotic canal
pte	pterotic
pts	pterosphenoid
ptss	pterosphenoid shelf
qf	quadrate foramen
qu	quadrate
rme	external mandibular ramus of trigeminal nerve
rmi	internal mandibular ramus of trigeminal nerve
RT	*retractor tentaculi* muscle
so	supraoccipital
sp	sphenotic
spo	supraoperculum
tcl	transcapular ligament
tco	temporal canal opening in sphenotic
v1	1st vertebra
vc	vertebral column
vo	vomer
vtp	vomerine tooth patch pedestel

ANATOMICAL DESCRIPTIONS OF *BELODONTICHTHYS* AND COMPARISONS WITH OTHER MEMBERS OF THE SILURIDAE AND SILUROIDEI

Neurocranium (Figs 2–12)

In dorsal view the cranium is oblong, its lateral margins are straight without any noticeable protrusions (Figs 2, 3). The mesethmoid is wide with a deeply rounded indentation in the midline of its anterior border. The mesethmoid cornu is broad, and posteriorly is widely separated from the lateral ethmoid. The lateral ethmoid is deep medially with a round, ventrolaterally directed palatine articular surface. Posteromedially it meets the anterior border of the frontal and posterolaterally extends beneath the frontal to meet the anteriorly extended margin of the sphenotic.

The vomer has a laterally expanded head, the anterior part of which is angled upward against the axis of the parasphenoid; posteriorly, the vomer has a long shaft (v, Fig. 2B) which terminates beneath the anterior part of the pterosphenoid. The vomerine tooth patch pattern is variable. In our specimens of *B. dinema* from Thailand, the tooth patches are small, transversely aligned and, widely separated with two or three teeth borne on a long bony pedestal (vtp, Fig. 2B). In specimens from Indonesia, the tooth patch is continuous with ca 10 teeth, supported on a thin bony flange (Fig. 2C). Bornbusch (pers. comm.) has observed continuous tooth patches in specimens from Thailand.

The frontals are deeply concave in both transverse and longitudinal planes, their medial borders rise to join one another in the form of a deep crest (fc, Figs 2, 4). The anterior fontanelle is short and entirely enclosed by the frontals and elevated between the paired frontal crests. The posterior fontanelle (pf) is narrowly separated from the anterior one (af) and has the appearance of a small foramen; it too is enclosed by the frontal crests (Figs 2, 4). Ventromedially, the frontals slope toward the midline where they meet the orbito- and pterosphenoids. Laterally each frontal is bordered partially by the sphenotic, posteriorly by the pterotic and medially by the supraoccipital (so, Figs 2, 3).

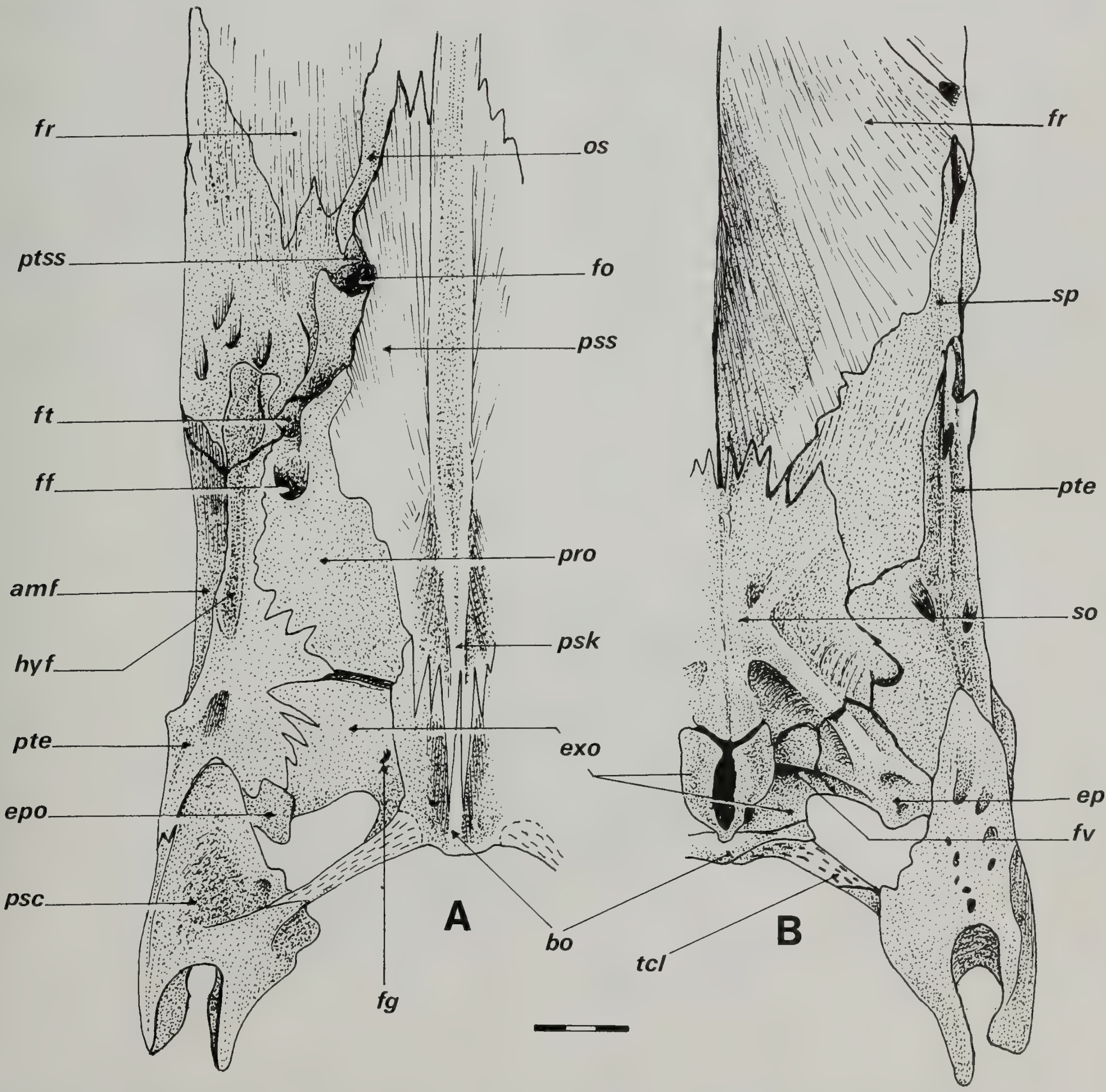

Fig. 3 *Belodontichthys dinema*: posterior part of neurocranium in A, ventral and B, dorsal views (LILI 89008).

The frontal sensory canal is short and runs diagonally from the anterior fontanelle to the anterior border of the bone where it meets the nasal canal. Owing to the trough-like contour of the anterior part of the frontal the course of the canal is strongly curved. A posterior branch of the canal extends from the posterior fontanelle and follows a diagonal course to the posterolateral border of the bone where it forms a tripartite connection with the infraorbital and temporal canals (lfc, Fig. 2A).

The sphenotic (sp., Fig. 3B) borders the posterolateral margin of the frontal but anteriorly is separated by that bone from the lateral ethmoid. Ventrally, the sphenotic contains the anterior part of the hyomandibular fossa. The cranial surface of the pterotic is concave, its raised lateral margin bearing the sensory canal. Posteriorly the border of the pterotic is indented where it meets the posttemporosupracleithrum; medially it contacts the supra- and epioccipitals; its ventral surface contains two long fossae, the upper for the origin of the *adductor mandibulae* muscle, the lower for the articulation of the hyomandibular (dmf hyf, Figs 3, 5).

The supraoccipital is a large anteriorly sloping bone that bears a shallow medial crest is continuous with that of the frontal; the semicircular canal tube is raised well above the bone's surface and runs posterolaterally to join the similarly elevated canal tube of the square-shaped epioccipital (epo, Figs 3B, 5). The exoccipital contributes to the dorsal surface of the cranium between the supra- and epioccipitals; posteriorly it is perforated by an extensive vagus foramen and posteromedially rises to border the supraoccipital (Fig. 6A). Its ventrolateral face is perforated by the glossopharyngeal foramen (fg, Fig. 3B). The basioccipital is short with a slight median keel (bo. Figs 3, 5); its exposed lateral surface is joined to the ventral (ligamentous) limb of the posttemporosupracleithrum. The only part of the basioccipital exposed dorsally is that forming the rim of the vertebral articular condyle which has an oblate outline (Fig. 6A).

Both the orbito- and pterosphenoids are shallow plate-like bones, the former contacting the frontal dorsally, the latter, both the frontal and sphenotic; ventrally the bones are sutured with the parasphenoid. The pterosphenoid is perforated centrally by the optic foramen which has a cowl-like dorsal shelf, and posteriorly its border forms part of the trigeminal foramen (ptss, Figs 3A, 5).

The prootic is a somewhat bullate bone, its anterior border forming the lateral part of the trigeminal foramen (ft). Lying close to the margin of that opening is a separate foramen for the hyomandibular branch of the trigeminal nerve trunk (Figs 3A, 5).

The parasphenoid has a marked ventral keel and its orbital part is angled upward relative to the vertebral axis. Ventral to the pterosphenoid the parasphenoid has a lateral, shelf-like expansion (pss, Fig. 3A). The otic part of the bone is broadly expanded to contact the prootics and the keel is continued posteriorly to the basioccipital (psk, Figs 3A, 5).

Comparisons

The neurocranium of *Belodontichthys* differs in several respects from that of other members of the Siluridae. The most marked of the differences are the sharply angled ventral surface of the vomer-mesethmoid, the keel-like and upwardly angled parasphenoid, the cavernous nature of the frontals and the modification of the sensory canals in the frontals.

The upward slope of the mesethmoid and thick cornua are otherwise only found in *Ompok* and *Wallago* (Fig. 7); in other silurid taxa the ethmoid has a horizontal ventral surface and narrow, pointed cornua with, in most *Kryptopterus* and all *Silurus* species examined, a slight posterior curvature (Fig. 8B). In *Hemisilurus* and *Kryptopterus moorei* the cornua are straight. The large, ventrally directed palatine articular surface of the lateral ethmoid of *Belodontichthys* is a feature also shared with *Ompok* (Fig. 8A). In *Wallago* and *Silurus*,

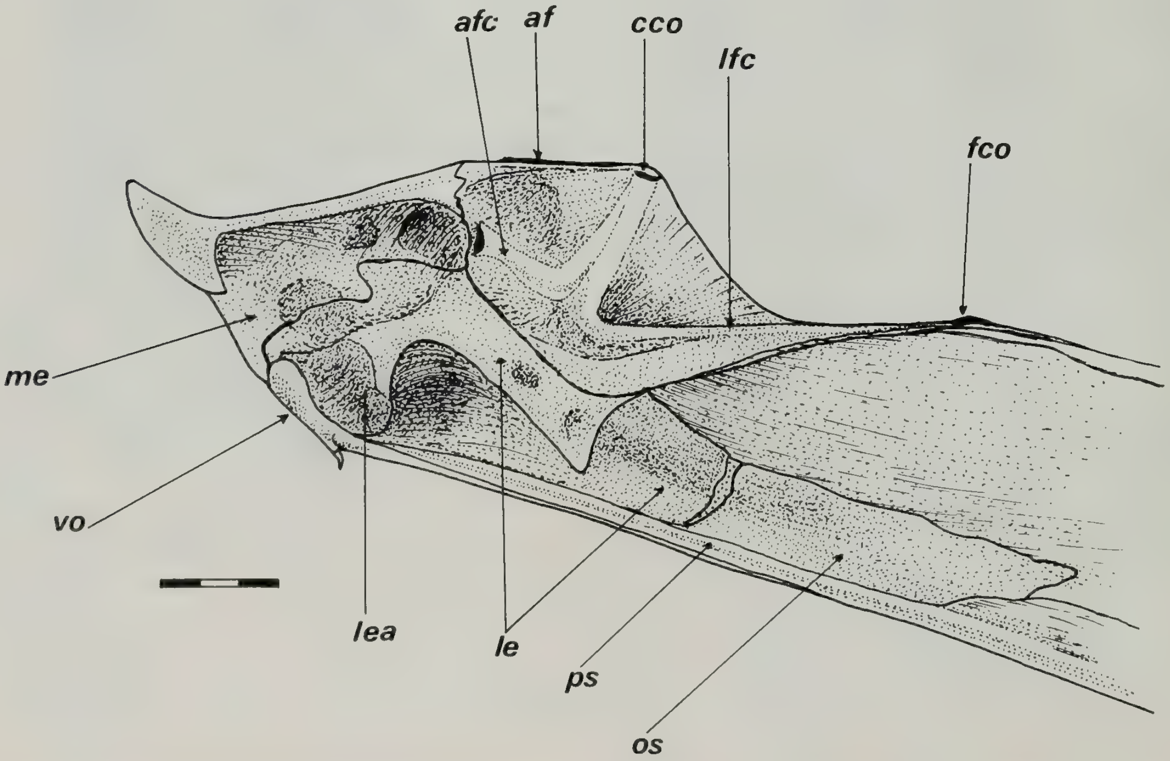

Fig. 4 *Belodontichthys dinema*: ethmoid region in left lateral view; shown in correct orientation relative to vertebral axis (LILI 89008).

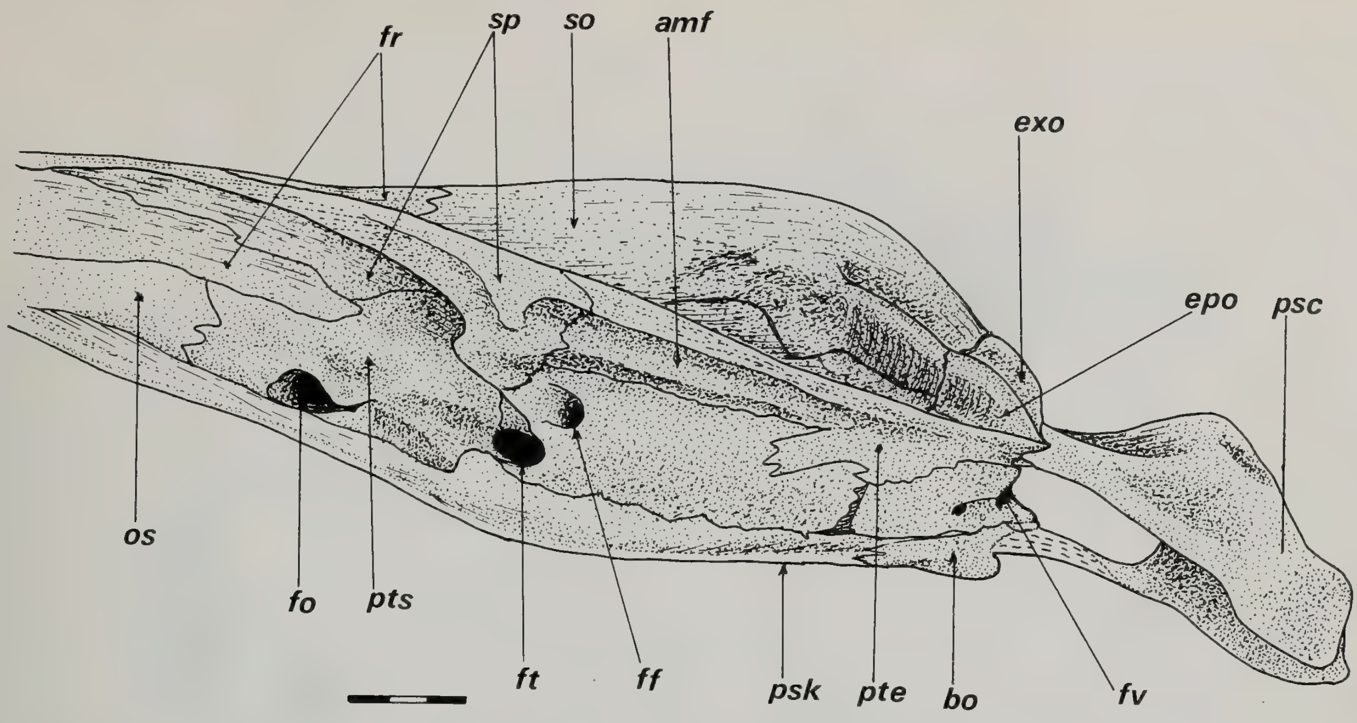

Fig. 5 *Belodontichthys dinema*: posterior part of neurocranium in left lateral view with posttemporosupracleithrum attached; shown in correct orientation relative to vertebral axis (LILI 89008).

although this articular surface is large, it is directed anterolaterally while in other silurid taxa it is small and situated laterally (Fig. 8B), i.e., the widespread and assumed plesiomorphic siluroid condition (Arratia, 1987; Bornbusch pers. comm.). The ventrally directed articulatory facet of the lateral ethmoid in *Belodontichthys* and *Ompok* is thus taken to be synapomorphic for these two taxa.

In its narrow head and upwardly sloping anterior surface, the vomer is also like that of *Ompok* and *Wallago*, however, in the latter genus the anterior border of the vomer is triangular rather than straight. A straight anterior border to the vomer is present in *Hemisilurus* and *Kryptopterus moorei. Ompok bimaculatus* resembles *Belodontichthys* in having narrow, transverse tooth patches bearing teeth carried on a bony flange (Fig. 8A). In some species of *Silurus* and *Kryptoperus* the vomerine tooth patch forms a continuous curved band but in *Wallago* and other *Silurus* species the band is V-shaped and interrupted in the midline to form two separate patches (Joseph, 1958; Kobayakawa, 1989).

Among siluroids vomerine tooth patches occur either paired or as a single, usually crescentic, band on either side of the vomerine head. Which of these conditions is the more derived is difficult to determine since both have equal distribution in the (admittedly restricted) number of taxa we have examined. Large, paired tooth patches occur in assumed plesiomorphic siluroids (Diplomystidae, Arratia, 1987; Hypsidoridae, Grande, 1987). Since vomerine teeth do not occur in other otophysans, out-group comparison does not aid in polarity assignment. Ontogenetic evidence suggests that the paired condition might be the more plesiomorphic since in post-larval *Clarias gariepinus* (which have a continuous band of teeth in adults) we have examined paired ossification centres precede the development of the teeth. In the largest specimen of the ontogenetic series examined (28mm SL) the tooth-bearing patches are still separated medially. We therefore suspect that the separated tooth patches represent the plesiomorphic siluroid condition (see also Bornbusch & Lundberg, 1989, fig. 6). Nonetheless, we also consider the reduced, transverse and pedestal-like process to be derived states of the vomerine tooth-patch type shared by *Belodontichthys* and *Ompok*.

No other silurid (or even siluroid) possesses the deeply concave frontal morphology of *Belodontichthys* but a partial excavation (concavity) of the posterior part of the frontal occurs in *Ompok* and *Wallago*. These latter genera also resemble *Belodontichthys* in having a short and narrow anterior fontanelle and high frontal crests. *Belodontichthys* is, however, unique in having the fontanelle entirely enclosed by the frontals and not extending anteriorly into the ethmoid. In *Belodontichthys* and *Ompok* the crest declines posterior to the fontanelle and becomes continuous with the supraoccipital crest (Figs 4, 7). In *Wallago* the crest remains elevated and in other members of the Siluridae takes the form of paired ridges which gradually rise from their origin to border the posterior fontanelle before meeting the supraoccipital crest.

Normally in siluroids the frontal sensory canal (supraorbital canal) runs along the medial part of the bone, diverging anteriorly to terminate where the nasal contacts the anterior border of the frontal. Posteriorly, the canal bifurcates, its medial branch (termed cross-commissure or parietal branch) enters the depression that lies between the anterior and posterior fontanelles and either opens in a pore or remains enclosed in the bony epiphysial bar which communicates with its contralateral partner. The lateroposterior branch joins the temporal canal of the sphenotic, *viz.* the plesiomorphic condition as exemplified in Diplomystidae (Arratia, 1987). In the Siluridae, the cross-commissure enters a channel formed between the raised frontal crests and there is no lateroposterior branch. Instead, an anterolateral branch extends forward to open on the frontal border above the centre of the orbit. The upper infraorbital bone appears to have a subcutaneous connection with this anterolateral branch as well as the temporal canal (Figs 9, 10). In *Silurus, Silurichthys* and *Kryptopterus* this branch of the canal is moderately divergent from the medial frontal canal but in *Wallago* the canal extends transversely from the midline (Fig. 9A) and in *Ompok* is curved posteriorly to form a crescentic ridge across the frontal (Fig. 10A).

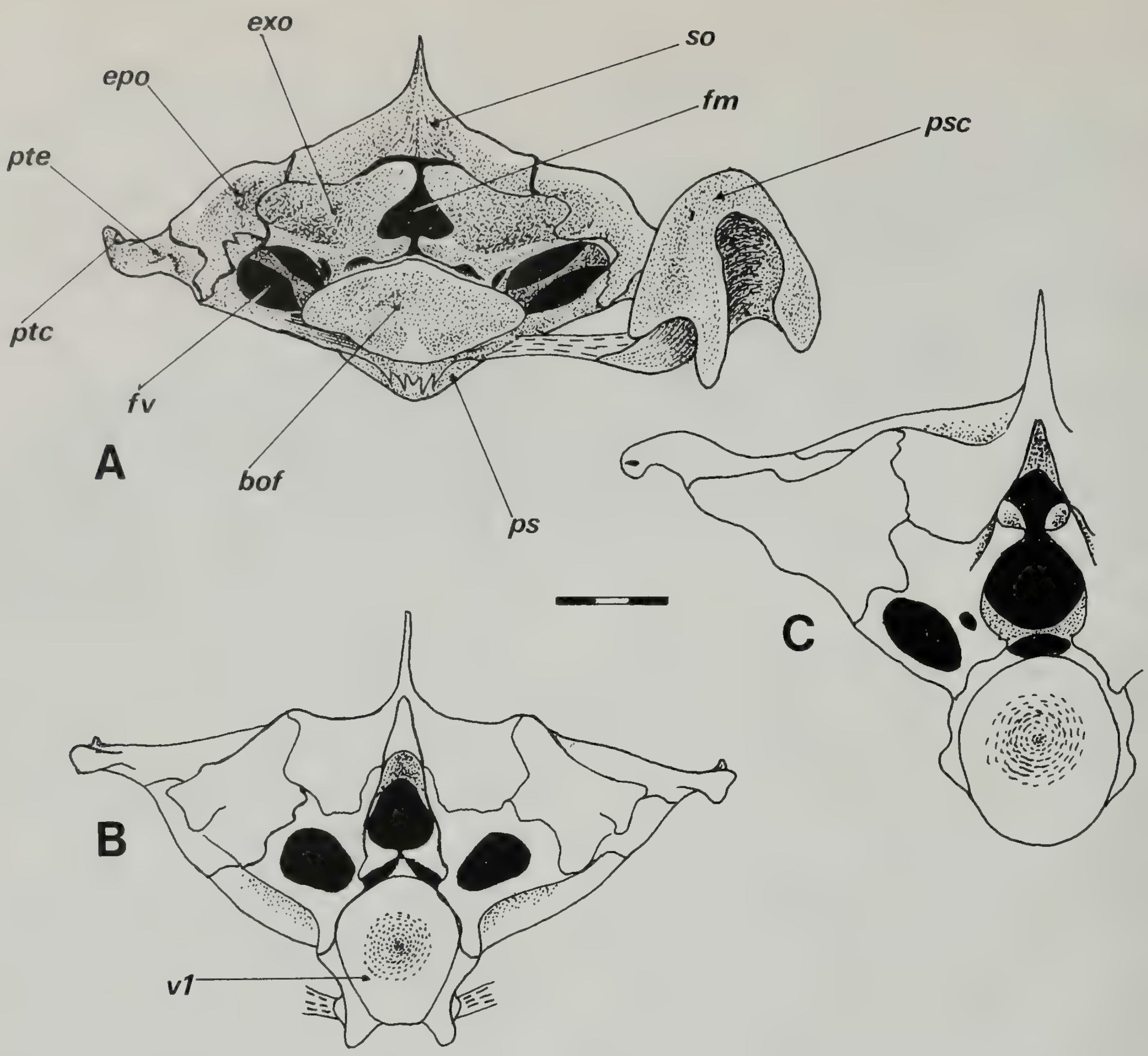

Fig. 6 Neurocrania in posterior view of A, *Belodontichthys dinema* (LILI 89008); B, *Ompok bimaculatus* (1891.11.20:171–8); C, *Wallago leeri* (1880.4.21:203).

In *Belodontichthys*, the canal branch extends posterolaterally, having a reversed orientation relative to that of other silurids but nonetheless still retains the lateral pore opening in the same position, *viz* midway along the edge of the frontal and above the orbit, the opening interconnecting with those of the sphenotic and infraorbital canals (see above and Fig. 2A). The lateroposterior orientation of the canal branch in *Belodontichthys, Ompok* and *Wallago* we consider as a shared derived state (see further discussion on p. 155).

In *Belodontichthys* the sphenotic is separated dorsally from the frontal by the lateral ethmoid, but the bones are in contact ventrally (Figs 2A, B). In other silurids examined the entire anterior margin of the frontal contacts the lateral ethmoid, a condition (first noted by Regan, 1911) not encountered elsewhere in siluroids and one considered synapomorphic for the Siluridae (Bornbusch, 1988; 1990). Kobayakawa (1989) figures the frontal in *Silurus mento. S. cochinchinensis. S. grahami and S. microdorsalis* as forming the lateral orbital border of the cranium, at least dorsally; if this is so, then the distribution of this character is incongruent with others shown in her cladogram of relationships. Bornbusch (pers. comm.) notes that there is variability within silurid taxa with respect to the degree of dorsal exposure of the frontal along the orbital margin.

The raised lateral border of the pterotic in *Belodontichthys* is a feature shared with *Ompok*. In both those taxa the sensory canal comes to lie along the 'medial' surface of the elevated border (Fig. 6A, B). In *Silurus* and *Wallago* (Fig. 6C) the pterotic border is also slightly raised but in other genera the border and its associated sensory canal remains flat. *Hemisilurus* is exceptional in that it too has an elevation of the pterotic, but here the canal runs lateral to the elevation which can thus be considered as a ridge rather than the pterotic margin.

The narrow orbital keel of the parasphenoid with its sharp midline ridge meeting the basioccipital (Figs 5, 7) are derived features (*Belodontichthys* shares only with *Ompok* among other examined silurids. In other Siluridae, the parasphenoid keel is broad and flat but both *Silurus* and *Wallago* share with *Belodontichthys* and *Ompok* a lateral expansion of the parasphenoid keel which meets posteriorly a similar shelf of the pterosphenoid (pss, pts, Fig. 11B). In no other taxon is the parasphenoid as sharply angled with respect to the vertebral axis as in *Belodontichthys*, although a pronounced but lesser angle occurs in *Ompok* (Fig. 7).

In *Belodontichthys* and *Ompok* the pterosphenoid is deeply indented where it meets the prootic, and its anteroventral border is extended anteriorly to form a somewhat tube-like opening for the optic nerve (Figs 5, 7).

In siluroids there is usually only a single opening for the trigeminal nerve trunk (a siluroid synapomorphy). *Belodontichthys* shares with *Kryptopterus* and *Hemisilurus* the presence of a secondary foramen in the prootic, through which passes the hyomandibular branch of the VII cranial

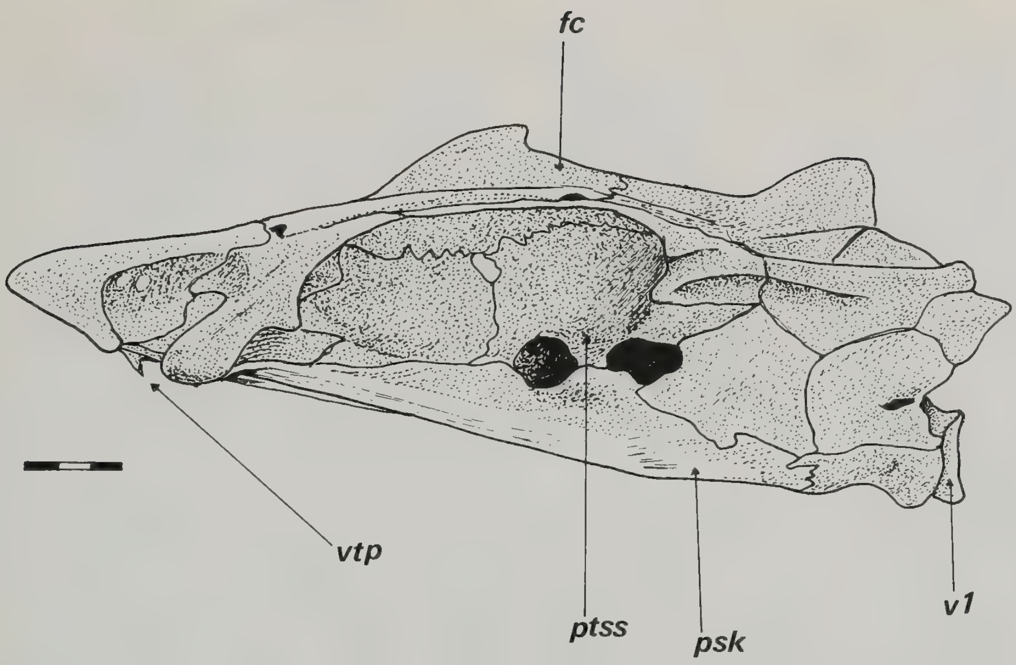

Fig. 7 *Ompok bimaculatus*: neurocranium in left lateral view (shown in correct orientation relative to vertebral axis); only those features of particular significance and discussed in the text are indicated (BMNH 1891.11.20:171–8).

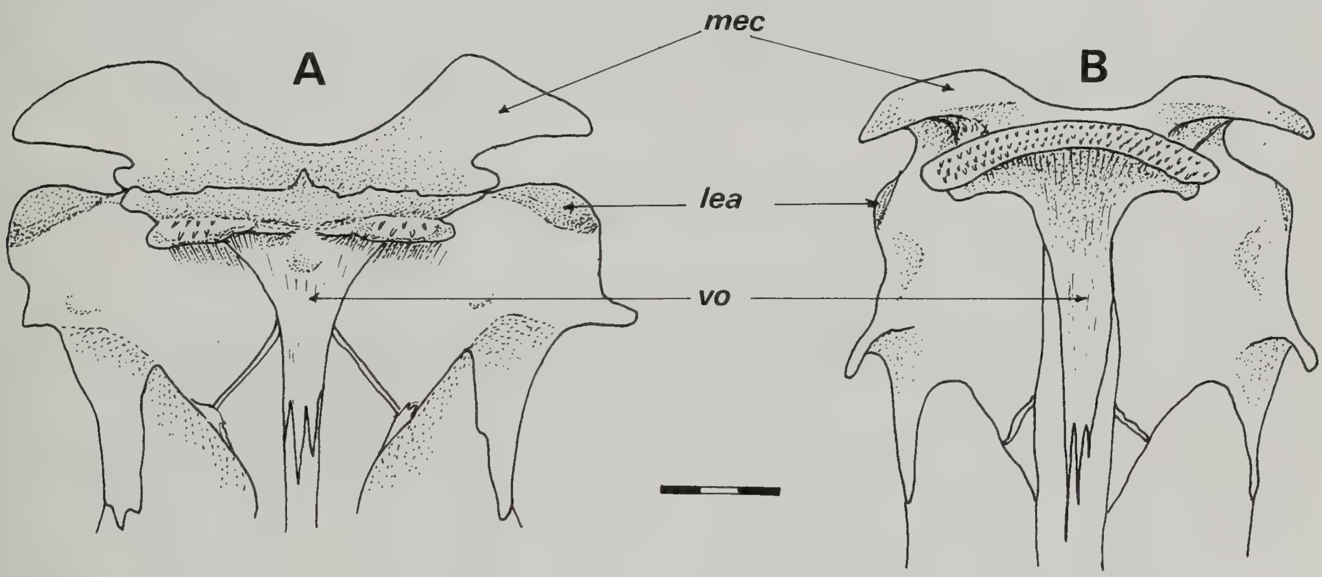

Fig. 8 Ethmoverine region in ventral view of, A, *Ompok bimaculatus* (BMNH 1891.11.20:171–8); B, *Kryptopterus bleekeri* (LILI 89030).

nerve (Figs 5, 12A). *Ompok* lacks this condition, as do other silurids investigated. *Silurus*, however, displays both conditions. In three specimens of *S. glanis*, one has a single trigeminal opening, although it is partially divided by a bony spur extending anterodorsally from the prootic (Fig. 12B), and two have a secondary foramen for the hyomandibularis nerve formed by a complete suture between a prootic process and the pterosphenoid (Fig. 12C). In *S. asotus* a prootic spur extends ventrally from the dorsal rim of the trigeminal opening (Fig. 12D). An accessory foramen for the hyomandibular branch of the trigeminal trunk also occurs in *Hypophthalmus* (Hypophthalmidae) (Howes, 1983:22) and has been reported in Pimelodidae by Lundberg *et al.* (1990). We have also found this condition in a specimen of *Chrysichthys cranchii* (Bagridae). The presence of an additional foramen in the prootic is considered to be a derived feature. In *Belodontichthys* as in other Siluridae the optic and trigeminal foramina are widely separated by a bony wall, but in *Hemisilurus* the separation is membraneous.

The occipital roof is somewhat flattened in *Belodontichthys, Ompok, Wallago* and *Silurus* but in *Hemisilurus* and *Kryptopterus* it is pinnacle-shaped. In all these taxa apart from *Silurus*, the epi- and supraoccipital semicircular canal tubes are elevated to form a high, posterior ridge to the cranial roof whereas in *Silurus* the canals are indicated only as slight ridges along the posterolateral margins of those bones. In all siluroids the exoccipital forms the lower posterior wall of the cranium; the lateral part of the bone lies in the transverse plane while the medial part turns at right angles to extend posteriorly beneath the supraoccipital. In the Siluridae the exoccipital, rather than being vertical as in the majority of siluroids, slopes backward so that it is visible from above. In all silurids other than *Silurus*, the dorsal part of the exoccipital is flat and contributes to the cranial roof. An apparent correlate of this arrangement is the reorientation of the vagus nerve foramen. Typically in siluroids the foramen perforates the posterior part of the lateral face of the bone. In *Silurus*, the foramen lies at the posterior margin of the bone (Fig. 11A); in other silurids it is located on the bone's posterior face and has the appearance of a posttemporal fossa. In *Silurichthys* and *Belodontichthys* the depression is extensive (Fig. 6A). The true posttemporal fossa in siluroids is a small cavity floored by the pterotic and roofed by the epioccipital, its opening usually occluded by the extrascapular and/or posttemporosupracleithrum. In Siluridae and Schilbeidae, however, a posttemporal fossa is absent (T.P. Mo pers. comm.).

The basioccipital is short in all Siluridae, its anterior ventral margin which contacts the parasphenoid, lying in line with the exoccipital-prootic suture and not as in many other siluroids lying beneath the centre of the prootic. The silurid condition may, however, be plesiomorphic since a short basioccipital occurs in Diplomystidae (Arratia, 1987). *Belodontichthys* appears unique amongst the members of the Siluridae in the oblateness of its basioccipital condyle (Fig. 6A).

In most silurids the medial arm of the posttemporosupracleithrum (transcapular) is compressed and well-ossified, but in *Kryptopterus, Wallago* and *Silurus* it has a long ligamentous connection to the basioccipital proximally *Belodontichthys* has an almost entirely ligamentous transcapular (Figs 3, 6). The posteroventral bifurcated portion of the posttemporosupracleithrum, into which the cleithrum fits is vertical in *Belodontichthys*, whereas in other Siluridae and the majority of siluroids it is directed somewhat laterally, as is the upright limb of the cleithrum; the *Belodontichthys* condition is reckoned to be the more derived. In common with other silurids, *Belodontichthys* lacks separate extrascapulars.

The jaws (Figs 13–16)

The maxilla is a long tapering bone with a transversely convex dorsal surface; its underside bears a longitudinal ridge (Fig. 13B, C). The head of the maxilla is flat, with double articulatory facets which contact the lateral border of the palatine. The premaxilla is angled at 45° to the midline; it is rather short and has a narrow dentigerous surface (Fig. 14A). The teeth are arranged in three irregular rows, the outer row teeth are the shortest and number 15–18, the inner and middle rows both number 9–10 and the teeth are nearly twice the length of those in the outer row, those of the innermost row being directed posteriorly. All the teeth have flattened, arrow-shaped tips (Figs. 14A).

The lower jaw is long, the length of the anguloarticular being 50% that of the entire jaw (Fig. 15). The dentary is shallow and rises posteriorly to form with the anguloarticular, a slight coronoid process. The dentigerous surface is narrow and bears three rows of teeth anteriorly and two rows posteriorly, the middle row extends only a short way along the surface. The outer row teeth number 16–18 which are short anteriorly but long posteriorly. The inner row teeth number 14–20, are markedly elongate and inwardly curved and long anteriorly and short posteriorly. The middle row teeth number 9–18 and are the same size as the anterior inner row teeth and, like them are recurved. All the dentary teeth have arrow-shaped tips. The dentary has a deep, anteriorly

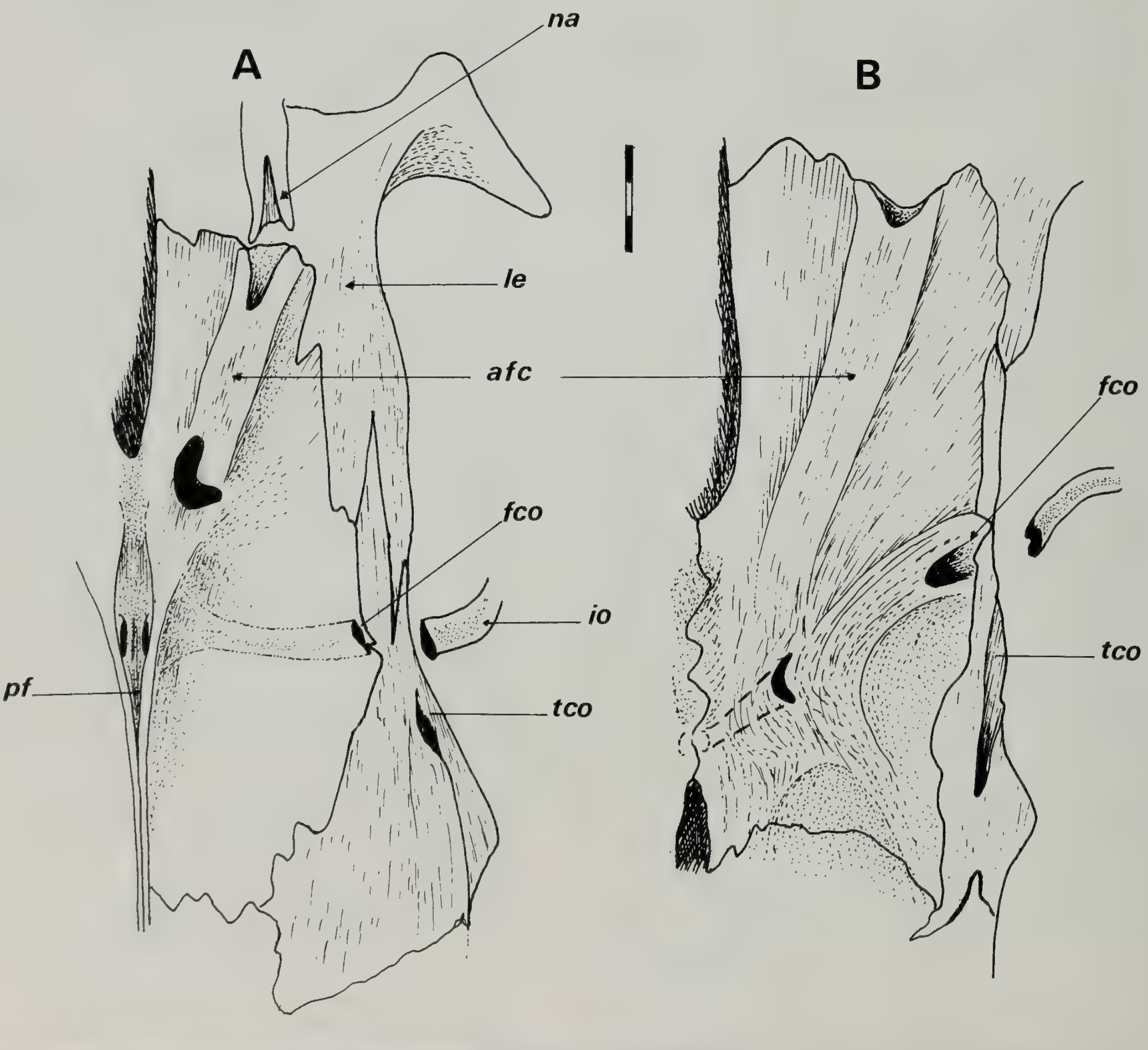

Fig. 9 Frontal and temporal sensory canals in A, *Wallago attu* (BMNH Uncat.); B, *Silurus glanis* (BMNH Uncat.).

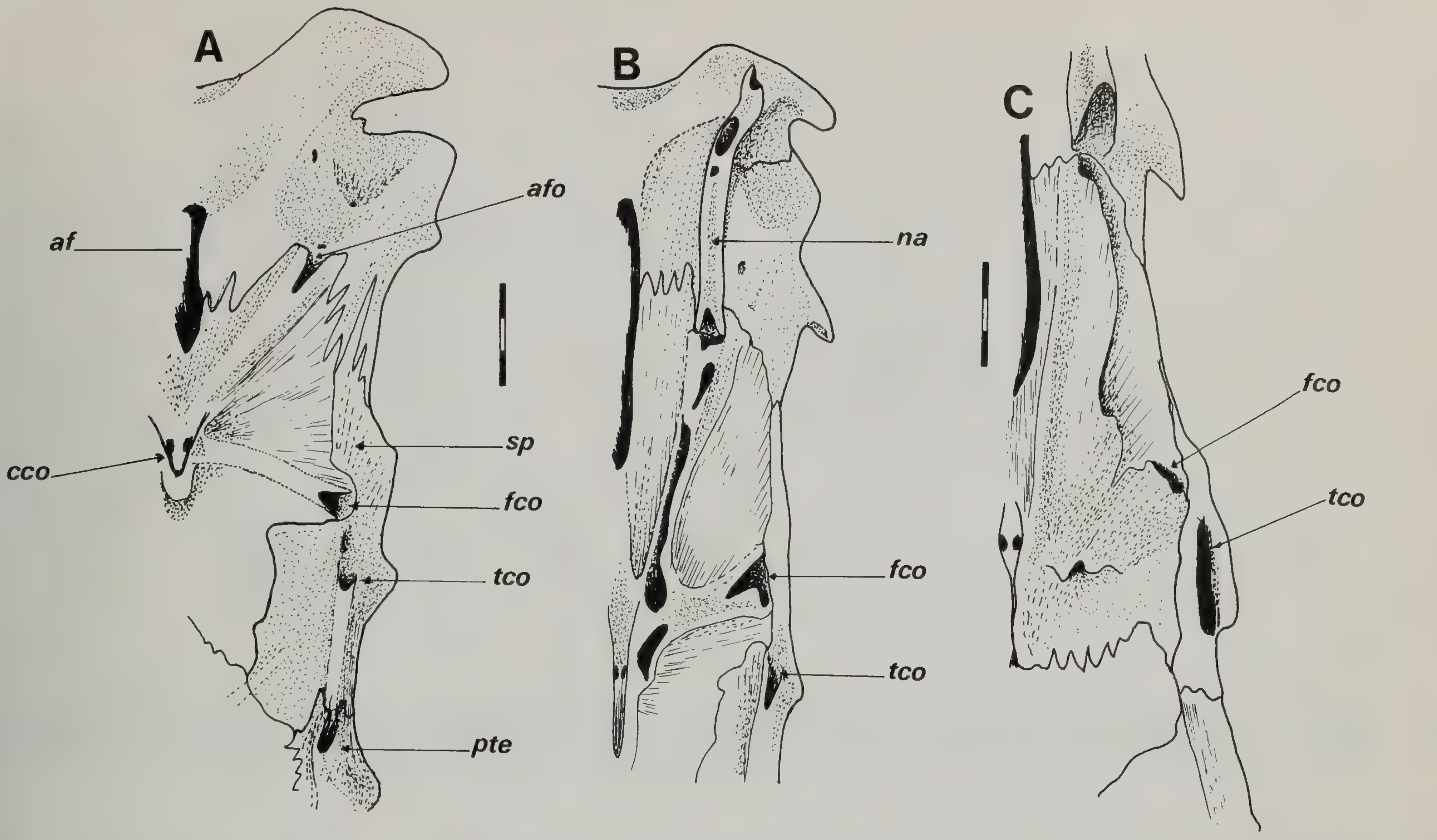

Fig. 10 Frontal and temporal sensory canals in A, *Ompok bimaculatus* (BMNH 1891.11.20:171–8); B, *Kryptopterus bleekeri* (LILI 89030); C, *Hemisilurus heterorhynchus* BMNH 1982.3.29:161.

extended mentomeckelian cavity; a small coronomeckelian bone lies in the posterior cavity of the anguloarticular from which the Meckelian cartilage extends forward. The anguloarticular is deep, its dorsal border lying at the same level as that of the dentary, forming a smoothly rounded coronoid process. The anterior border of the anguloarticular extends well forward into the mentomeckelian cavity of the dentary. The articulatory surface is complex, with a large, inwardly angled facet (Fig. 15C).

In keeping with the condition in other members of the Siluridae and the majority of siluroids examined, the premaxilla of *Belodontichthys* is approximately half the length of the lower jaw. The laterally exposed surface, i.e. the part not covered by the ethmoid cornua, is 45% of its total length. In comparison, the exposed surface in other silurid taxa ranges from 25% (*Kryptopterus apogon*) to 40% (*Ompok bimaculatus*). The premaxillary ascending process, which contacts the lateral margin of the ethmoid cornua, is a rather prominent, obliquely transverse process in *Belodontichthys* and *Ompok*, whereas in other Siluridae it rises gently to a promontory situated in the centre of the bone (Figs 14A–D).

The lower jaw of *Belodontichthys* differs markedly from that in other genera of Siluridae and the majority of siluroids in having only a slight inward curvature at the symphysis (Fig. 15D); in other taxa the united rami form a broad crescent or a U-shape. The dentary differs little in its length and depth from that in other Siluridae and, like most, has 5 openings in the sensory canal. *Silurus* and *Wallago* have between 6 and 10. The dentary canal openings in *Hemisilurus* and *Ceratoglanis* (Bornbusch & Lundberg, 1989) are extensive and separated from one another by narrow bony struts (Fig. 16C). The moderate development of the coronoid process of *Belodontichthys* agrees with that in most siluroids. According to Lundberg (1970) and Grande (1987) an elevated coronoid process is the more derived siluroid condition. However, a high process is also present in Diplomystidae (Arratia, 1987), and among the Siluridae a reduced coronoid process appears to be a derived condition associated with increased jaw length (i.e. *Silurus* and *Wallago*). The articular surface of the anguloarticular in all genera of the Siluridae apart from *Wallago* and *Belodontichthys* bears a transverse facet which in these two genera is obliquely angled. No other silurid taxon has such a complex articular surface as *Belodontichthys* (Fig. 15C).

In all members of the Siluridae, apart from *Belodontichthys, Ompok* and *Kryptopterus moorei*, the dentigerous areas of the jaws are broad, the teeth ranging from short, stout and conical (*Hemisilurus, Silurichthys*) to long and caniniform, the most derived state being exemplified by *Belodontichthys* (see above). A series of elongate inner row teeth is a feature shared not only with *Ompok, Silurus* and *Wallago* but also with two *Kryptopterus* species, *K. micronema* and *K. kryptopterus*. In these latter taxa, however, the elongate teeth are widely separated from each other by three or four uniformly sized smaller teeth whereas in the other three genera all the teeth are elongate and regularly spaced. Of the other *Ompok* species we have examined, *O. pabda* is the only one, apart from *O. bimaculatus* which has equally sized elongate inner-row teeth. We assume this condition to be synapomorphic for *Belodontichthys, Ompok* (in part), *Silurus* and *Wallago*. On the basis of the different condition of the irregularly spaced teeth in *Kryptopterus* and the incongruence of other synapomorphies (p. 153) we hypothesise that the *Kryptopterus* condition is independently derived.

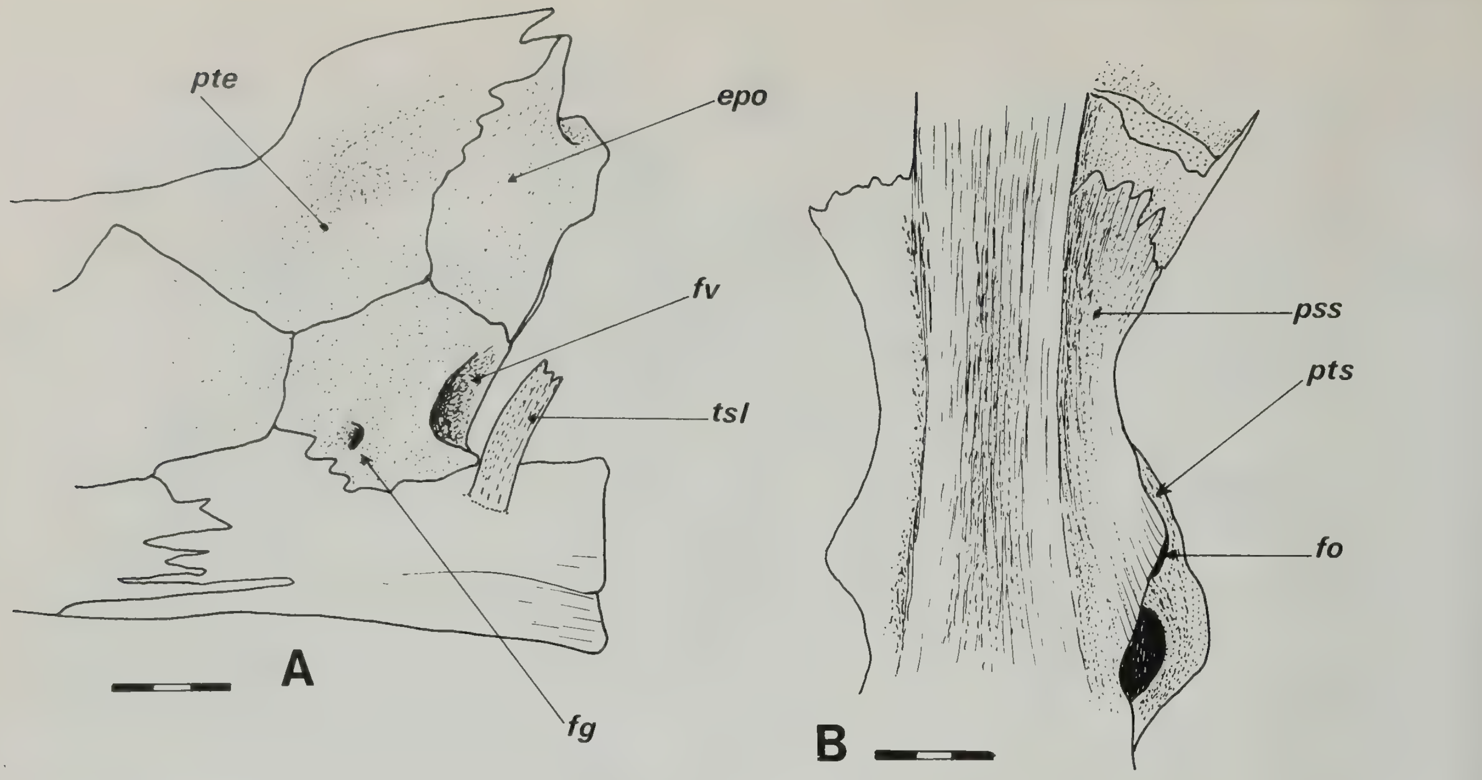

Fig. 11 A. *Silurus asotus*: posterior part of neurocranium in lateral view showing position of vagus foramen (transcapular ligament cut); B, *Silurus glanis*: orbital region of parasphenoid in ventral view to show shelf (BMNH uncat. specimens).

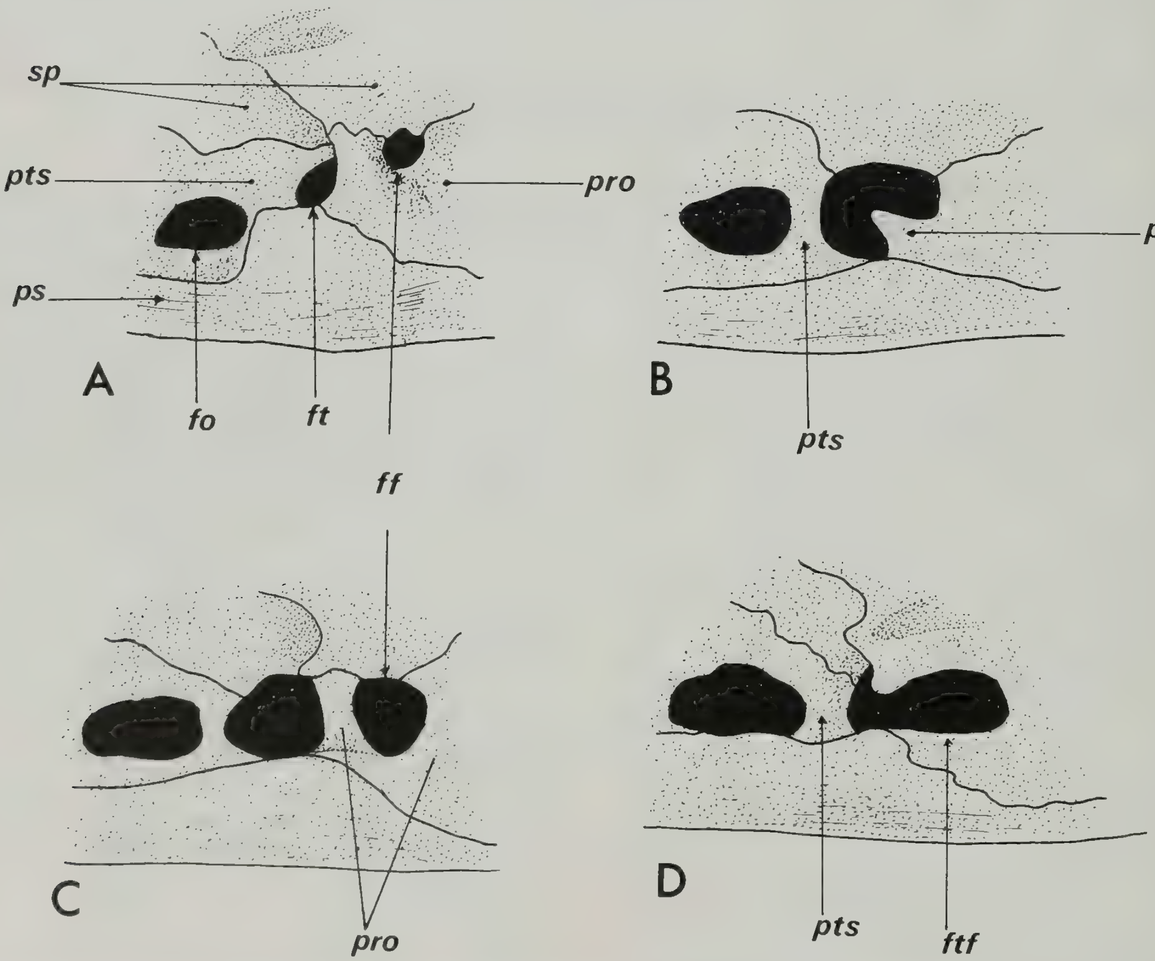

Fig. 12 Trigeminal and facial nerve foramina in A, *Kryptopterus bleekeri* (LILI 89016); B, *Silurus glanis* (114mm cranial length); C, *S. glanis* (105mm CL); D, *S. asotus* (65mm CL; all BMNH Uncat.).

Hyomandibular and palatoquadrate (Fig. 17)

Relative to the condition in other genera, the hyomandibular is somewhat higher than broad, has a horizontal dorsal articulatory surface, and an irregularly concave anterior border. A strong vertical crest with a concave anterior border extends down the anterolateral face in front of the hyomandibularis nerve foramen (Fig. 17A). Posteriorly, there is

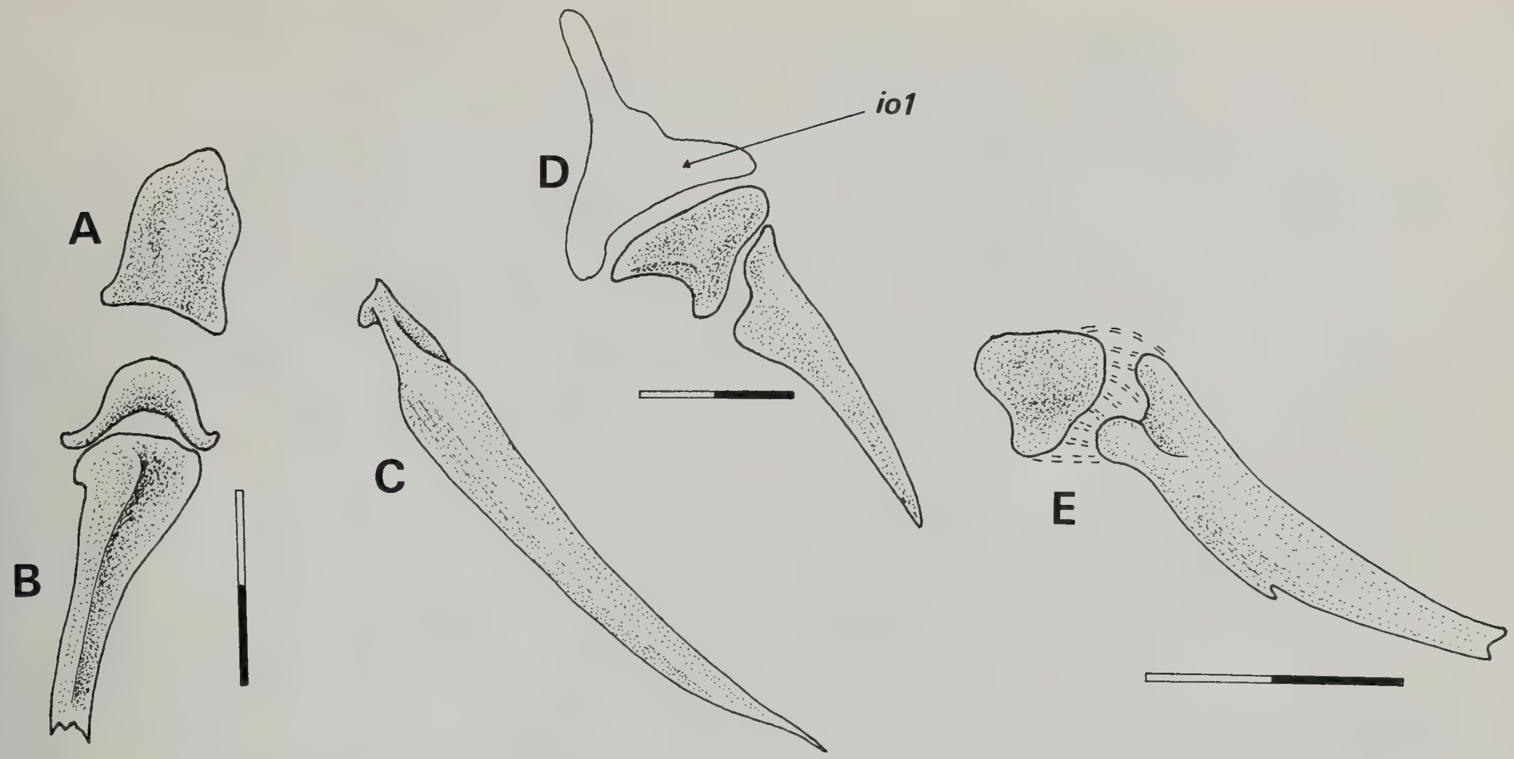

Fig. 13 *Belodontichthys dinema*: A, palatine (right) in dorsal view; B, palatine and maxillary head (anterior view of articulation); C, maxilla (right) in lateral view (LILI 89002); D, *Ompok bimaculatus,* palatine with maxilla (right), shown *in situ* with respect to 1st infraorbital (BMNH 1891.11.20: 171–8); E, *Wallago attu,* palatine and maxilla (right) in articulation and bound by connective tissue (double-dashed lines) LILI 89074.

a well-developed opercular condyle; ventrally, the bone is indented by the foramen for the mandibularis branch of the hyomandibular nerve and is covered by the properculum. The quadrate is large with (in cross-section) a triangular articular condyle whose articulatory surface is deeply divided (Fig. 17A). The posteroventral surface of the quadrate is covered by the lower part of the preoperculum. There are two pterygoid bones, an extensive posterior element which contacts, respectively, the anterior and dorsoanterior margins of the hyomandibular and quadrate, and a small, oblong element ligamentously suspended between the large pterygoid and the lateral ethmoid (ppt and apt, Fig. 17A).

Comparisons

Compared with other members of the Siluridae, *Belodontichthys* has a narrower hyomandibular with a more pronouncedly concave anterior border. The longitudinal lateral crest also has a marked concave anterior margin and its ventral surface serves as the site of insertion for the *levator arcus palatini* muscle and origin of the inner section of the *adductor mandibulae* muscle. A prominent longitudinal LAP crest also occurs in *Ompok* (Fig. 17E) but in other Siluridae apart from *Wallago* it is reduced to a narrow bar. In *Wallago attu* the width of the crest is such that it extends forward as a long pointed lamina of bone to overlap the posterolateral face of the large pterygoid (Fig. 17E), whereas in *W. leeri* the crest is much narrower and more closely resembles the condition in *Silurus* (Fig. 17C, D). Generally, in siluroids, if a lateral crest or ridge for the insertion of the LAP occurs at all, it is horizontal or subhorizontal (Lundberg, 1970; Grande, 1987) and we have found a similar vertical ridge to be present only in the schilbeids, *Proeutropiichthys* and *Eutropiichthys*. According to Bornbusch (1990) the vertical crest in Siluridae is not homologous with the horizontal (LAP) crest in other siluroids since it serves principally as the site of adductor muscle origin. As noted above, however, the LAP crest is sometimes subhorizontal and also acts as an area of attachment for the adductor musculature. Thus it seems to us that the vertical ridge or flange in Siluridae is a reorientated LAP crest. As such this feature is considered synapomorphic for the Siluridae and the enhanced development of the crest in *Belodontichthys, Ompok* and *Wallago* is taken to represent a further derived condition for these taxa (see also under quadrate).

The dorsal articular surface of the hyomandibular in siluroids almost always bears an anterior process which articulates with the sphenotic; the size and degree of medial tilt of the process are variable (Lundberg, 1970). In the Siluridae, however, the anterior dorsal process is, apart from *Silurus*, reduced (Bornbusch, 1988). *Silurus* retains the plesiomorphic condition in which the process is large and almost vertical (Fig. 17D). The specimens of *Belodontichthys* and *Ompok bimaculatus* that we have examined lack a dorsoanterior process, although a small cartilaginous process is present in a cleared and stained preparation of the former and a minute, medially directed process is present in other *Ompok* species examined.

The large, posterior pterygoid bone in siluroids is generally referred to as the metapterygoid. Since the homologies of this and the other pterygoid elements in siluroids have not been firmly established (Arratia, 1987; Howes & Teugels, 1989) we refer simply to posterior and anterior pterygoids. Only two pterygoids occur in Siluridae, the anterior of which is always reduced and is either situated distant from the anterior border of the posterior pterygoid (*Belodontichthys, Ompok*) or closely associated with it (other Siluridae; cf. Figs 17A, F and B, E); in either case it is ligamentously attached to both the posterior pterygoid and the lateral ethmoid. The shape and size of the anterior pterygoid is also variable and may be large and plate-like (*Wallago*), rod-shaped (*Silurus*) or a short, oblong lamina (other taxa); Figs 17B–E.

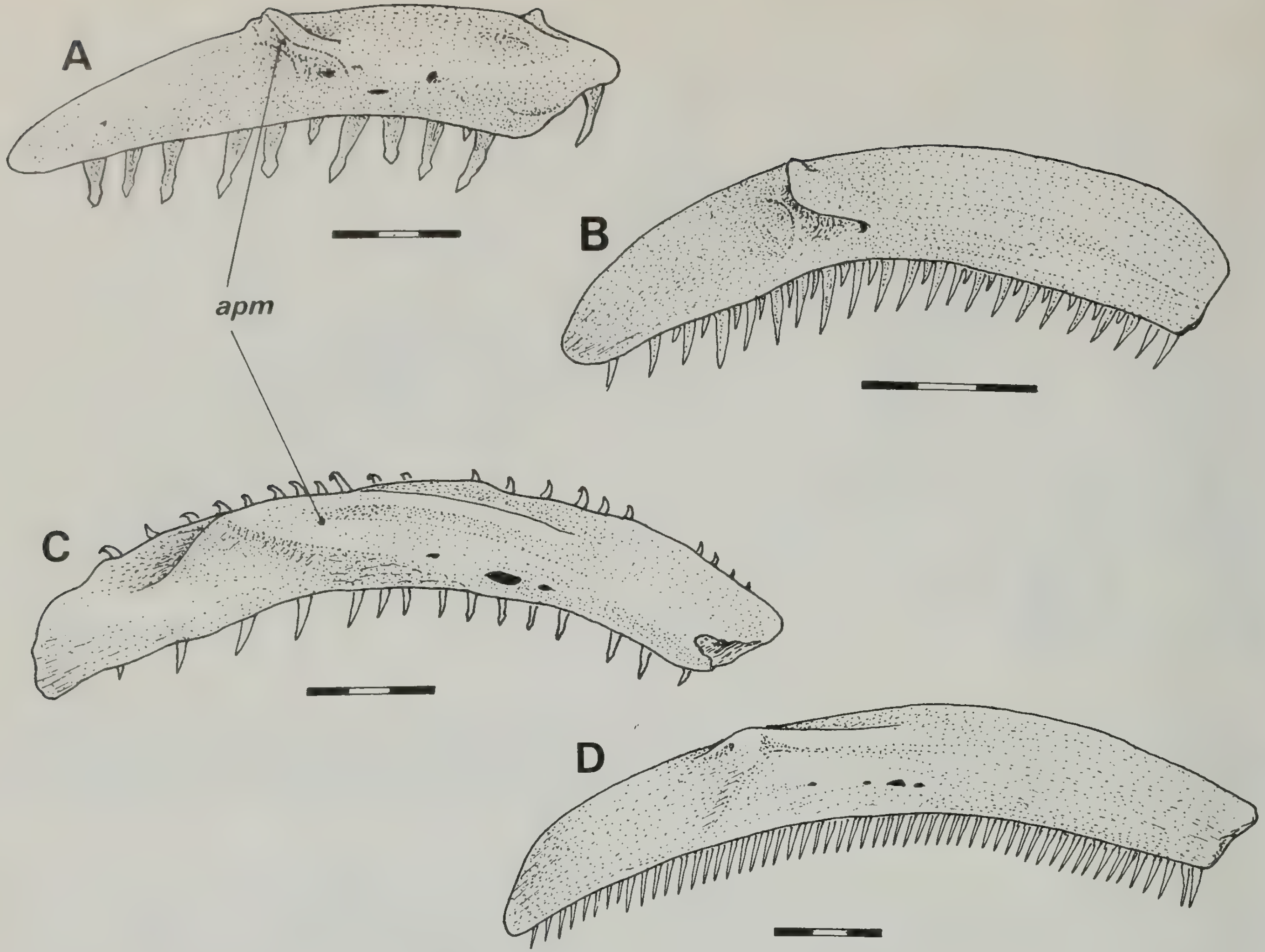

Fig. 14 Premaxillae (left): posterodorsal views of A, *Belodontichthys dinema* (LILI 89008); B, *Ompok bimaculatus* (BMNH 1891.11.20:171–8); C, *Kryptopterus apogon* (LILI 89016); D, *Wallago leeri* (BMNH 1880.4.21:203).

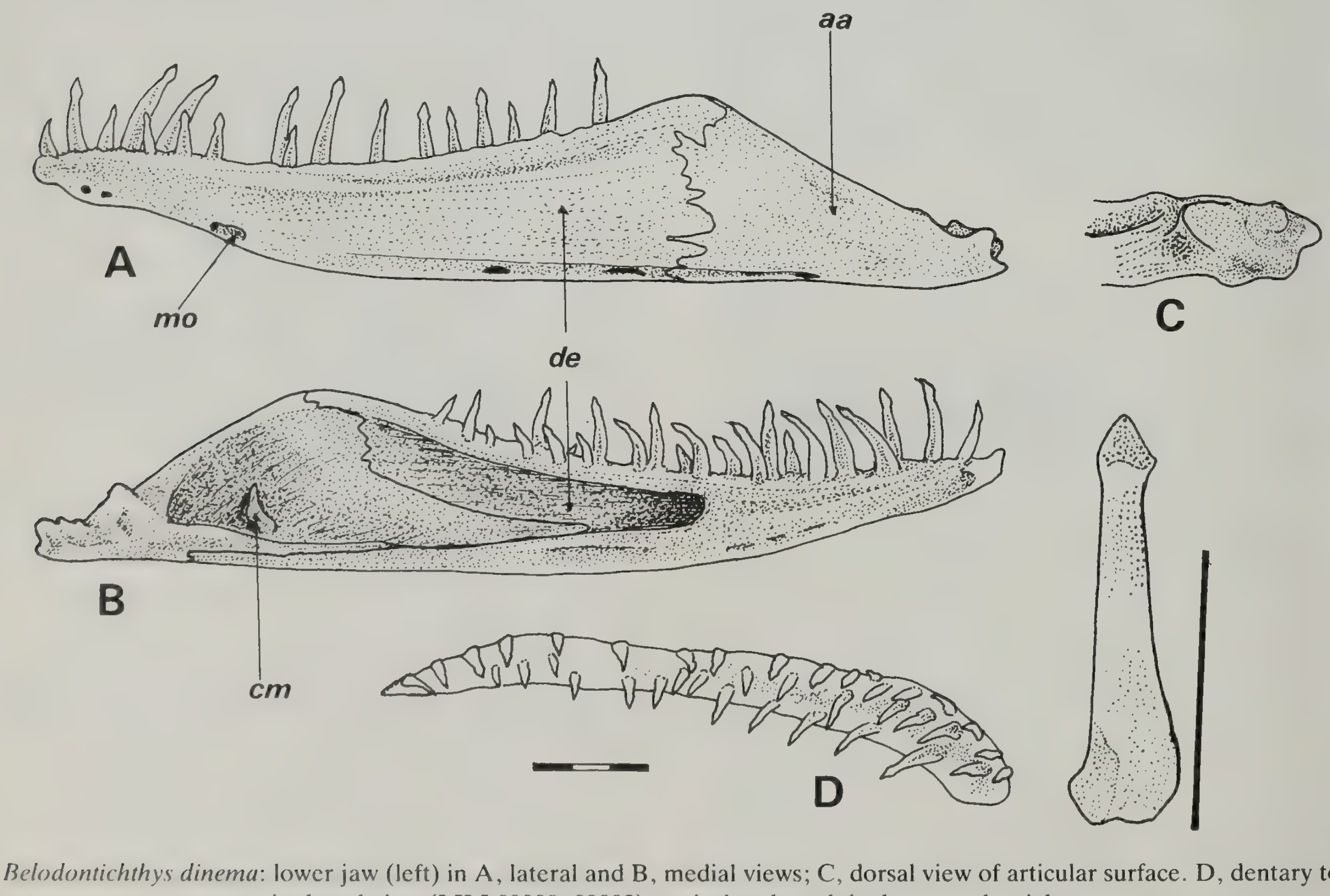

Fig. 15 *Belodontichthys dinema*: lower jaw (left) in A, lateral and B, medial views; C, dorsal view of articular surface. D, dentary tooth patch in dorsal view (LILI 89008, 89002); an isolated tooth is shown at the right.

The quadrate of *Belodontichthys* differs from that of other silurids in the form of its articular condyle (Fig. 17A). The condyle has two distinct articulatory surfaces which are deeply divided. In cross-section the entire condyle is triangular and has a slightly concave medial face. In other silurids there is a single, transverse articulatory surface which may bear a slight central indentation and which, in cross-section, is oblong with a straight or convex medial face (Figs 17B–F). The more complex articular surface of the *Belodontichthys* quadrate is correlated with the similarly complex articular arrangement of the lower jaw (see above).

Two other marked modifications of the quadrate occur within the Siluridae. In *Wallago attu*, the quadrate is deeply divided anteriorly in its saggital plane, the inner lamina contacting the posterior pterygoid and the hyomandibular dorsally, the outer lamina contacting the lateral laminate crest of the hyomandibular (Joseph, 1958; Fig. 17E). In effect, the division of the quadrate is a result of the ventral continuation of the LAP hyomandibular crest (see above). The precursor of this condition is evident in *Wallago leeri* and *Silurus asotus* where there is a prominent lateral process of the quadrate in line with that of the hyomandibular (Figs 17C, D). In *Silurus glanis* the process is present but weakly developed; it also appears to be present in *S. aristotelis* and *S. microdorsalis* but is absent in *S. torrentis* and *S. cochinchinensis* (Kobayakawa, 1989). The second derived feature of the quadrate occurs in some *Kryptopterus* species where the anteroventral part of the bone is perforated by a large foramen (Fig. 17B). No vessel passes through the aperture and it probably acts as an expansion cavity for the adductor musculature. The foramen is present in *K. bleekeri* and *K. apogon* but not in any other *Kryptopterus* examined. A similar, but smaller foramen also occurs in *Wallago attu*. *Ompok bimaculatus* and *Hemisilurus heterorynchus* (Figs 17E, F). The ventromedial surface of the quadrate, posterior to the articular condyle is excavated by a deep fossa in most Siluridae, and it would seem that further attrition of the outer wall could lead to the development of the foramen in these taxa. The presence of a fossa or foramen in the anterior ventral part of the quadrate is not an unusual feature in siluroids and the size of the fossa is correlated with that of the dorsal process of the anguloarticular which it accommodates.

In the Siluridae the palatine is a small hoof-shaped nodular element which, in *Belodontichthys* and *Ompok* is reduced by thinning to a helmet-like element (Fig. 13).

The maxilla articulates with the anteroventral surface of the palatine. As a consequence of the orientation of the palatine against the articular facet of the lateral ethmoid, the maxilla comes to lie in a sagittal rather than transverse plane (Fig. 13D). In no other siluroid is the palatine reduced to the extent of that in the Siluridae, but the similar shape, manner of articulation and overall reduction in size of the palatine in

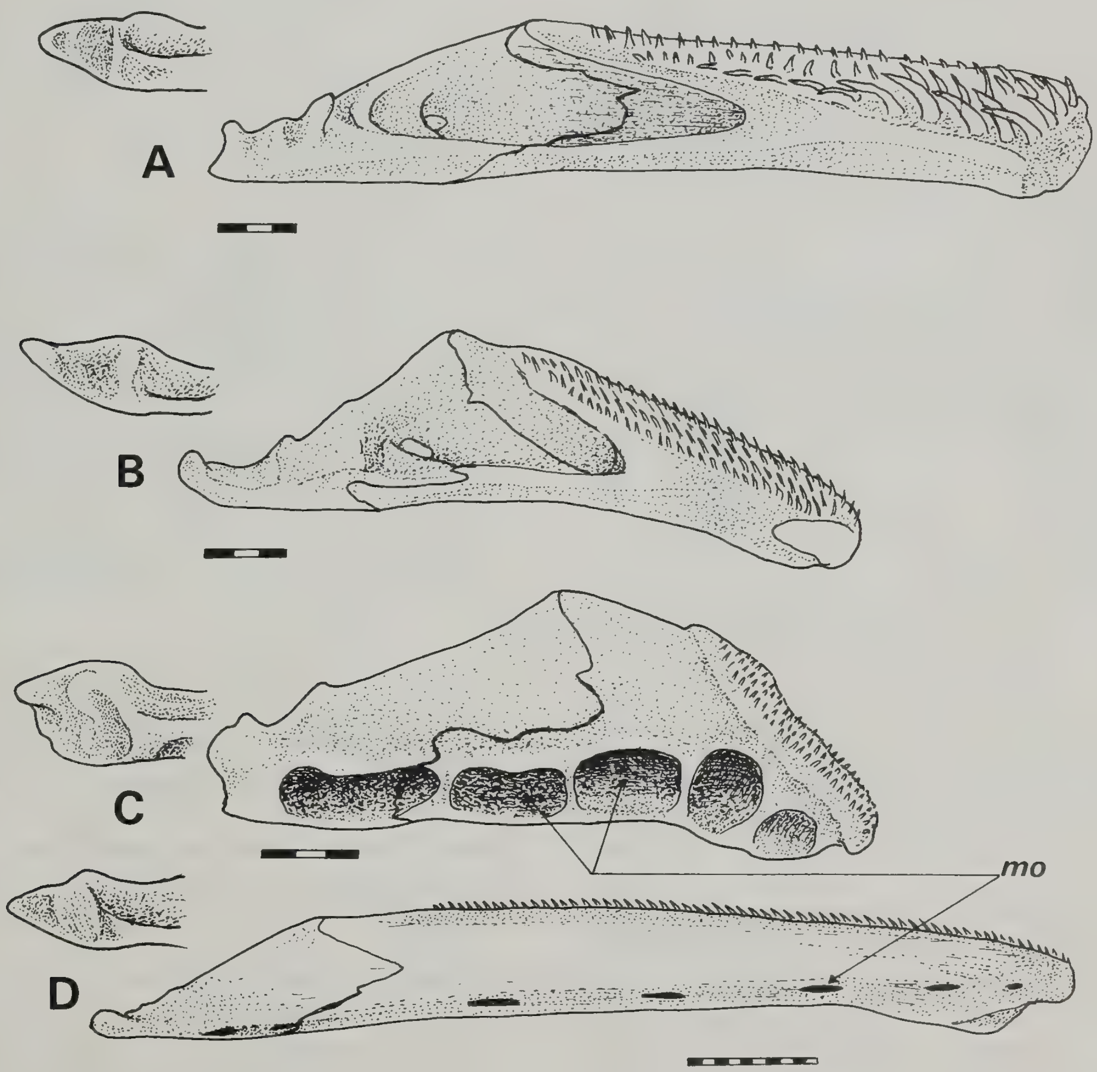

Fig. 16 Lower jaws of A, *Ompok bimaculatus*, medial view (BMNH 1891.11.20:171–8); B, *Kryptopterus bleekeri*, medial view (LILI 89030); C, *Hemisilurus heterorhynchus*, lateral view (BMNH 1982.3.29:161–2); D, *Wallago attu*, lateral view (BMNH Uncat.). The articular surfaces are shown at the left of each respective jaw.

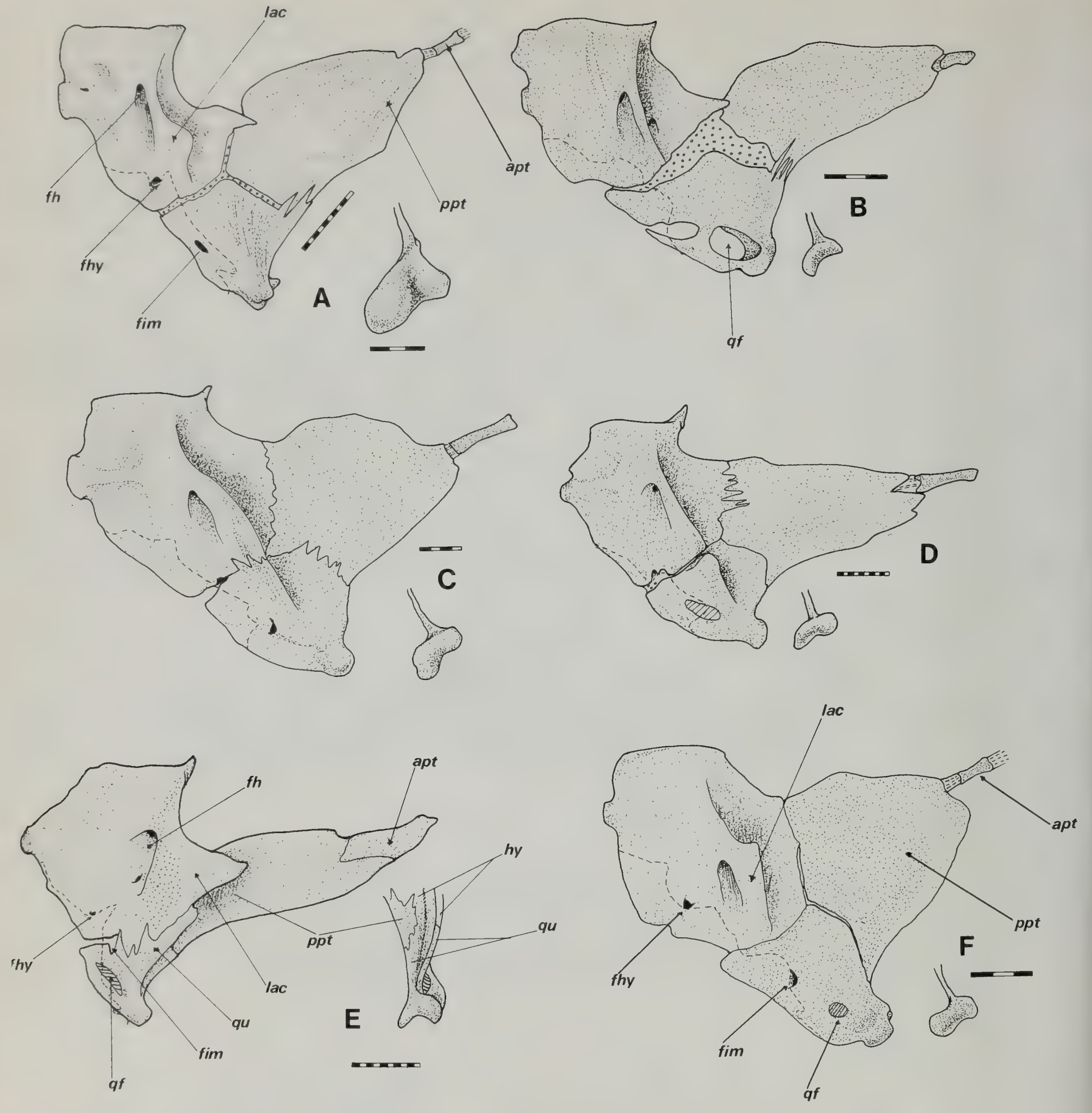

Fig. 17 Hyomandibular and palatoquadrate of A, *Belodontichthys dinema* (LILI 89008); B, *Kryptopterus bleekeri* (LILI 89030); D, *Silurus asotus* (BMNH 1880.4.21:203; E, *Wallago attu* (BMNH Uncat.), F, *Ompok bimaculatus* (BMNH 1891.11.20:171–8); all in lateral view. The articular surface of the quadrate, as viewed anteriorly, is shown to the right; the dashed lines crossing the posterior margins of the hyomandibular and quadrate indicate the anterior margin of the preoperculum when in place.

Malapteruridae caused Howes (1985) to regard the condition as synapomorphic for the two families. Bornbusch (1990) has demonstrated the non-homologous nature of the silurid and malapterurid palatine reductions and we follow him in regarding the reduced, nodular element of the Siluridae as synapomorphic for the family. The palatine in the Siluridae appears to be a single ossification and is considered as an autopalatine; in other siluroids, the posterior extension of the bone is probably the dermopalatine.

Myology (Figs 18–26)

The *adductor mandibulae* is an extensive muscle covering the entire postorbital region, its fibres separated dorsally by the *levator arcus palatini* into lateral and medial elements (Fig. 18). Posteriorly, the lateral element stems from the rim of the preoperculum and the posterolateral face of the hyomandibular, and dorsally from a long pterotic fossa (Fig. 5); its insertion is on the outer rim of the anguloarticular. The lower part of the lateral element originates from the ventral region of the hyomandibular and quadrate; these fibres insert on an aponeurosis medial to the anguloarticular. From this aponeurosis the mandibularis section of the adductor (Aw) extends to fill the deep mentomeckelian cavity of the dentary. The medial element of the *adductor mandibulae* extends from the lower, anterior region of the hyomandibular and the posterior pterygoid bone. From there its fibres run ventrolaterally to insert aponeurotically with the outer element medial to the anguloarticular. The mandibularis branch of the trigemino-facialis nerve runs vertically across the face of the inner element, identifying the latter as the A2 division (Howes, 1983*b*).

Anteriorly, two large triangular muscles originate from the anterior pterygoid element. The lower inserts principally (and musculously) on the dorsoanterior border of the premaxilla, but a small dorsal bundle of fibres inserts tendinously onto the base of the maxilla. The upper element, whose fibres intermesh at their origin with those of the *adductor arcus palatini*, inserts partially on the small, helmet-shaped palatine and partially on the base of the maxilla. The upper element is identified as an *extensor tentaculi*, the lower as a *retractor tentaculi* (Figs 18, 19).

The *adductor arcus palatini* is a well-developed muscle extending the length of the parasphenoid and inserting along the medial margin of the pterygoid series (Fig. 19). Posteriorly, the muscle thickens, extends onto the lower part of the prootic and inserts broadly across the medial face of the hyomandibular; this segment is the *adductor hyomandibularis*.

The *levator arcus palatini* muscle (LAP) is a large, pyramidical element originating from the sphenotic, its fibres inserting *via* a thick tendon onto a laminar process rising vertically from the anterior rim of the hyomandibular (Figs 18, 19).

The *dilatator operculi* (DO) is an extensive, bipinnate muscle. Its anterior fibres originate from the lateral ethmoid; the main body of the muscle from the frontal, and its posterior fibres from the sphenotic. The lateral fibres run towards the central tendon at a 45° angle whereas the medial fibres lie almost parallel to the tendon. Since the frontal is deeply concave the DO lies almost vertically with the lateral and medial fibres orientated dorsally and ventrally to the central tendon. The muscle crosses the face of the LAP, passing behind the outer layer of the adductor mandibulae and the dorsal tip of the preoperculum to insert on the anterodorsal process of the operculum (Figs 18, 19).

Both the *levator* and *adductor operculari* muscles are small, triangular elements having their origins, respectively, from the ventrolateral rim and ventral surface of the pterotic. Their insertion is across the upper medial face of the operculum, that of the adductor overlapping the posterior half of the levator (Fig. 18).

The *epaxialis* muscle extends as far forward as the anterior margins of the frontals (Figs 20, 21). Above the cranium, the muscle is a single mass undivided by a medial septum or containing any myocommata. Only posteriorly, behind the supraoccipital, does the muscle become divided in the midline by the septum stretching from that bone to the 1st neural spine.

Comparisons

Among other silurids, the *adductor mandibulae* morphology of *Belodontichthys* most closely resembles that of *Ompok, Wallago* and *Silurus* (Figs 20, 21). In all these taxa the outer element (A1) is extensive, almost square-shaped, with a near vertical anterior border and straight dorsal border. The posterior origin of the muscle is from the supra- and preopercular bones, and its dorsal origin from the margin of the pterotic, in common with other silurids. In contrast, however, the pterotic margin is hidden, the lateral fibres of the epaxial muscle appearing contiguous with those of the *adductor*. The fibres of the inner element (A2) run ventrolaterally and almost vertically to their lower jaw insertion. The eye lies immediately lateral to A2.

In *Kryptopterus* (Figs 22, 24B) and *Hemisilurus* (Fig. 23) muscle A1 has a concave anterior border and a short dorsal origin from the pterotic, the margin of which visibly separates the epaxial from the adductor musculature. In *Kryptopterus bleekeri, K. apogon, K. moorei, K. limpok* and *K. cryptopterus*, the eye lies lateral to muscle A1 and the area of the muscle behind the eyeball is entirely tendinous. That tendinous sheet also provides a fascia for the fibres of muscle A2 which runs ventroanteriorly and obliquely to their lower jaw insertion. In *K. bicirrhis*, the muscle A1 is narrow crescent with only a few fibres inserting on the dorsal rim of the anguloarticular (Fig. 24A). The remainder of the muscle extends forward onto the lower jaw without the intervention of an aponeurosis to become continuous with Aw.

The arrangement of the *adductor mandibulae* musculature in the Siluridae is rather typical of that in the majority of siluroids; the insertion of the outer element on both dorsal and medial aspects of the anguloarticular is a plesiomorphic arrangement (Howes, 1983*a*). However, the tendinous region behind the eye in some *Kryptopterus* species is an unusual feature paralleled in the Hypophthalmidae (Howes, 1983*a*). The vertical orientation of the fibres of A2 in *Belodontichthys, Ompok, Silurus* and *Wallago* is also unusual but a similar situation is present in the schilbeid *Eutropiichthys* where the fibres run not only vertically but turn posteriorly to join a central tendon of the muscle (Fig. 25). In *Eutropiichthys* muscle A2 has a uniquely derived feature whereby it originates from the lateral ethmoid as well as the frontal and sphenotic and skirts the dorsal curvature of the eyeball (Fig. 24A).

In all Siluridae both *extensor* and *retractor tentaculi* muscles are present (Bornbusch, 1990). As in *Belodontichthys*, the extensor in other silurids is an elongate muscle, its anterior portion running obliquely from the lateral ethmoid to the palatine; its posterolateral portion extending from the orbital region. In *Kryptopterus bicirrhis* the extensor runs from the dorsal rim of the pterygoid whereas in other *Kryptopterus* it originates from the cranium, usually the orbitosphenoid, its fibres extending from a thin fascia covering the *adductor arcus palatini* (cf Figs 24A, B). In *K. apogon, K. bleekeri* and *K. limpok* the muscle fibres extend from the medial surface of the frontal (Fig. 23B) and in *Silurichthys*, the origin of the extensor covers the entire orbital face of the cranium (orbitosphenoid, pterosphenoid and prootic). In all silurids there is a dual palatine insertion of the *extensor*. Those fibres running from the lateral ethmoid inserting on the palatine's dorsal surface and lateral rim, while those extending horizontally from the orbital region insert on the bone's ventral surface and medial rim (Fig. 21B).

When present in other siluroids the *extensor tentaculi* originates principally from the lateral ethmoid and orbitosphenoid, the fibres being orientated from postero- to anterolaterally and often broadly inserting along the length of the palatine (in the majority of siluroids, the palatine is a

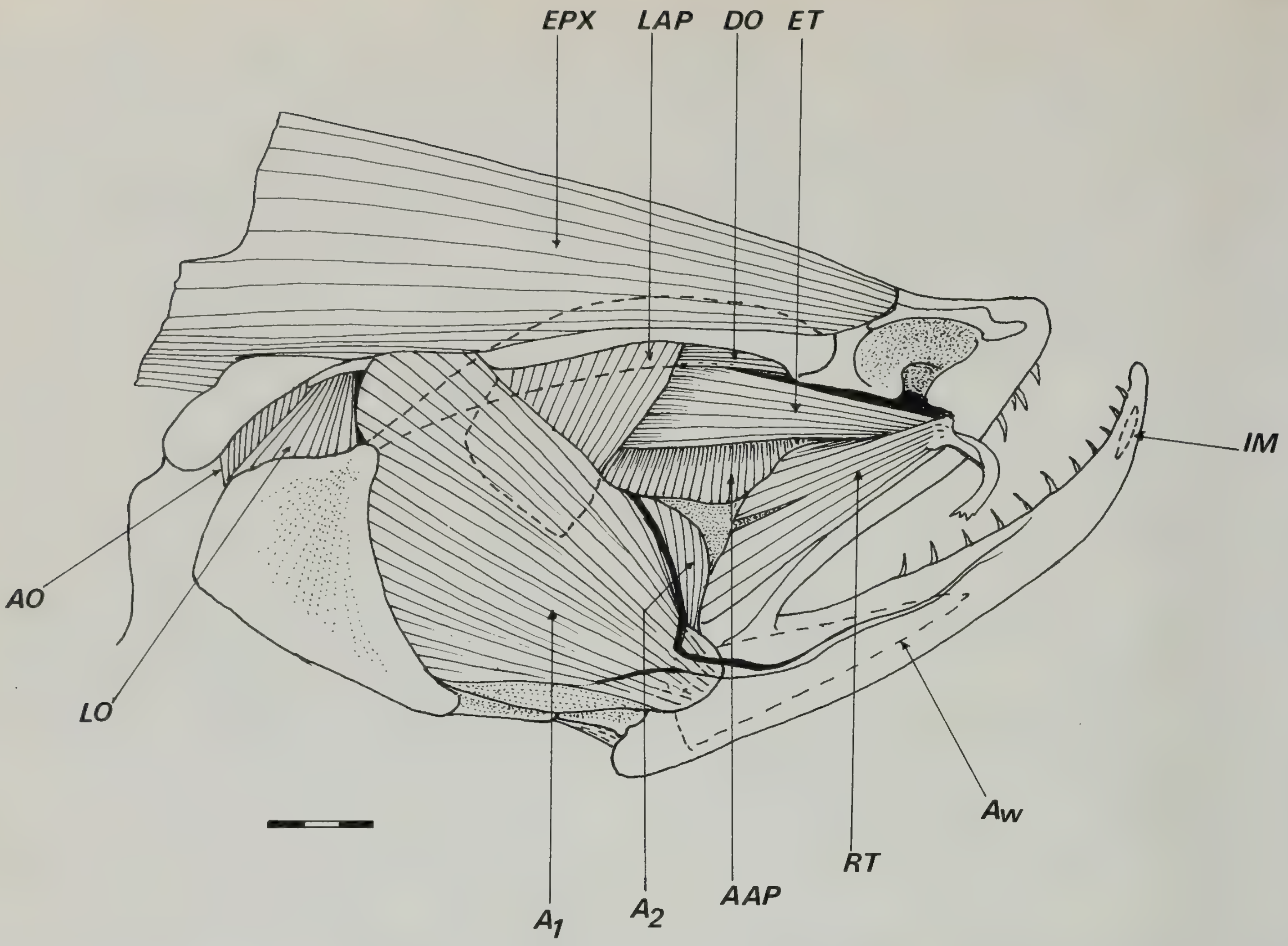

Fig. 18 *Belodontichthys dinema*: superficial cranial musculature; dashed lines indicate the underlying DO and LAP muscles (LILI 89002).

long, rod-shaped bone, unlike the nodular element of the Siluridae). Among other siluroids examined, only in Hypophthalmidae does the *extensor* run longitudinally from the rear of the orbit. In this case, however, the muscle originates from the body of the *adductor arcus palatini* along the dorsal border of the posterior pterygoid, whereas in silurids its origin covers a broad area of the posterior part of the *adductor arcus palatini* and encroaches on the parasphenoid, orbitosphenoid, pterosphenoid and, in *Wallago*, also on the sphenotic.

In most other silurids the *retractor tentaculi* originates from a connective tissue fascia covering the posterior pterygoid medial to muscle A2. In *Wallago*, as in *Belodontichthys* there are two distinct segments of the retractor, the upper of which inserts on the base of the barbel, the lower passing beneath the upper segment to insert at the midpoint of the maxilla (Fig. 21C). Only in *Kryptopterus cryptopterus* is there a connection of the extensor with the premaxilla as in *Belodontichthys*. *Belodontichthys* most closely resembles *Kryptopterus bicirrhis* in its relatively short retractor and in the muscle's origin from the anterior pterygoid. Bornbusch (1990) has pointed out that the length and orientation of the *retractor tentaculi* in most Siluridae is a probable correlate of the shortened palatine.

The distribution of a *retractor tentaculi* amongst siluroids has not been documented. Howes (1983*a*) drawing on a limited survey of Old and New World taxa, supposed that the muscle had been derived independently in several lineages. No evidence has emerged from this study to alter that opinion.

In all of the Siluridae, the *levator arcus palatini* (LAP) is extensive, originating from the sphenotic and (with the exception of *Kryptopterus bicirrhis*) from the posterior margin of the lateral ethmoid. The LAP inserts on the anterior margin of the hyomandibular and in *Ompok* and *Wallago*, as in *Belodontichthys*, the insertion area is a laminar projection of the bone (Fig. 17A). A large LAP is commonly encountered among siluroids (Howes, 1985), and is also present in the Diplomystidae.

In nearly all silurids the *dilatator operculi* (DO) is elongate and extends well forward onto the underside of the sphenotic and frontal. *Belodontichthys* shares with *Ompok, Wallago* and *Silurus* a lateral ethmoid origin of the muscle. In *Kryptopterus bicirrhis* and *Silurichthys* the DO is confined to the postorbital part of the cranium and its origin involves only the lateral part of the sphenotic. In *K. cryptopterus* and *K. limpok* the muscle originates further forward, from the orbital part of the sphenotic and in *K. apogon* and *K. bleekeri* from the frontal as well (Fig. 22B). In the two latter species, the DO lies flat against the underside of the frontal and the orbital portion of the sphenotic. It then turns abruptly into the vertical plane where it passes medial to the LAP. At this point, the lateral edge of the muscle is firmly attached to the sphenotic border by a tendon thus seemingly allowing only the medial aspect of the muscle free movement.

The morphology of the DO among siluroids is variable and that encountered in the Siluridae is not unusual. An elongate DO extending over the ventral surfaces of the frontal and sphenotic is a common condition amongst the Pimelodidae, Bagridae, Clariidae and Loricarioidei (Howes, 1983*a*), and a

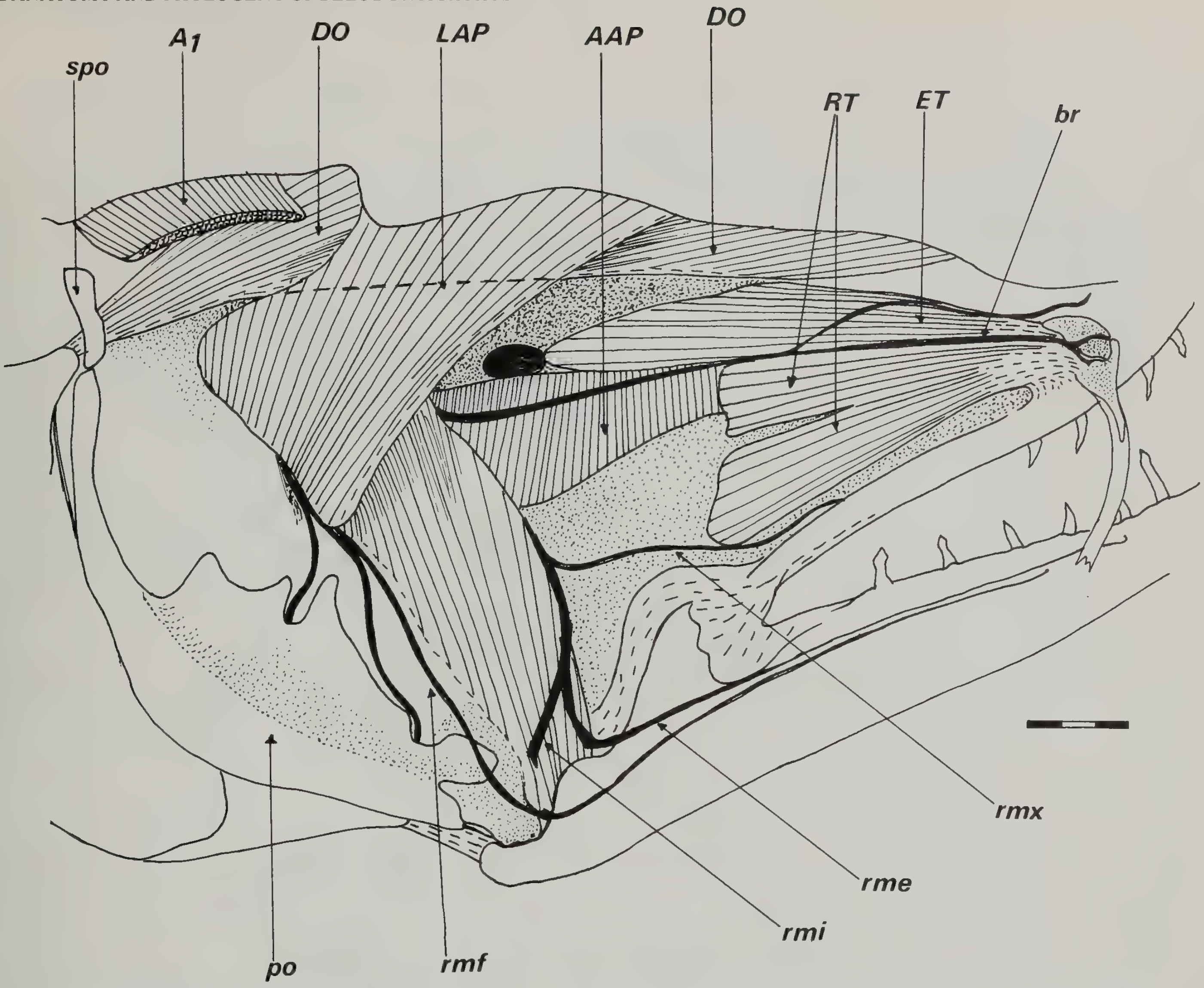

Fig. 19 *Belodontichthys dinema*: deeper cranial musculature. Muscle A1 is cut through; the lower border of DO is indicated by dashed line crossing LAP (LILI 89008).

large DO with a frontal origin occurs in the Diplomystidae. The presumed plesiomorphic condition of the DO (that which is regularly encountered in other ostariophysans) is present in *Ictalurus* where the muscle is small and vertically orientated, with its origin confined to the posteroventral region of the sphenotic.

The *adductor arcus palatini* (AAP) has a variable morphology in the Siluridae. The usual condition is for the muscle to run between the parasphenoid and the pterygoid bones, while posteriorly it covers the lower part of the medial face of the hyomandibular and is considered a separate element, *viz* the *adductor hyomandibularis* (Winterbottom, 1974). This condition occurs in *Belodontichthys, Hemisilurus, Silurus, Wallago, Silurichthys, Hito, Ompok, Kryptopterus bicirrhis, K. cryptopterus, K. limpok* and *K. moorei*. In contrast, in *K. bleekeri* and *K. apogon*, the AAP extends dorsally to cover the orbitosphenoid, pterosphenoid and medial part of the frontal. Only in Schilbeidae (*Schilbe*) where the AAP attaches to the frontal (Fig. 26) have we encountered a condition similar to that in the two cited *Kryptopterus* species.

In the other members of the Siluridae examined the epaxial musculature extends forward onto the frontal in *Silurus, Wallago, Ompok* and *Hemisilurus*. However, only in *Wallago* and *Ompok* does the musculature cover a large posterior area of the bone. In *Silurus* only a small region of the bone is covered and the anterior border of the muscle is marked by a strong transverse frontal ridge. *Hemisilurus* lacks the frontal concavity of the former taxa, the frontal being convex with the epaxial muscle inserting, as in *Silurus*, along a prominent frontal ridge. Like *Belodontichthys*, the supraoccipital crest in *Ompok* is reduced in height and does not divide the muscle bloc whereas in other silurids the muscle is divided in the midline by the crest.

In siluroids, the mandibularis branch of the trigeminal nerve usually follows a course across the junction of muscle A1 with the lower jaw (often penetrating through dense connective tissue), passes ventrally across the posterolateral face of the anguloarticular and then anteriorly along the sensory groove of the dentary to innervate the labial tissue. Along this latter part of its course the nerve is joined by the external branch of the hyomandibular nerve trunk which leaves the lower hyomandibular foramen and passes anteroventrally between muscles A1 and A2 then laterally across the mandibuloquadrate joint to run along the outer face of the lower jaw. This nerve pattern has been found in all the siluroids examined.

DISCUSSION

Derived characters shared by *Belodontichthys* with other Siluridae

In the preceding comparative analyses we have identified a number of derived characters possessed by *Belodontichthys*

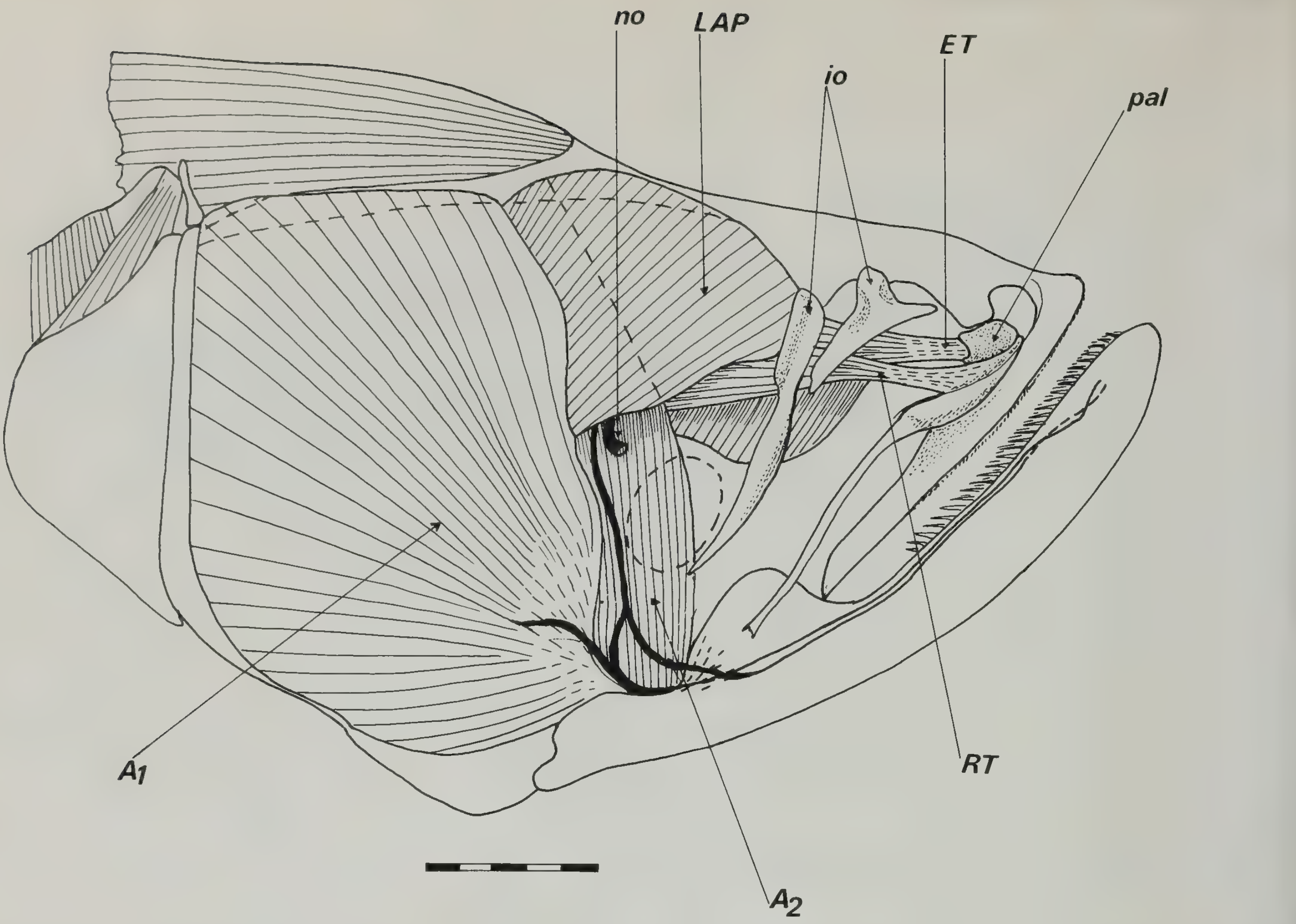

Fig. 20 *Ompok bimaculatus*: cranial musculature. Dashed lines indicate underlying DO and A2 muscles. The circular dashed line covering A2 muscle indicates the position of the eye (BMNH 1891.11.20:171–8).

and shared with other genera of the Siluridae. The monophyletic nature of the Siluridae has been shown by Bornbusch (1990) who recognises five synapomorphies. These are the reduced palatine; the occlusion of the frontal margin by the lateral ethmoid and sphenotic; the compression of the transcapular ligament of the posttemporosupracleithrum and the absence of dorsal fin radials and posterodorsally shifted anal fin pterygiophores. In addition to these synapomorphies we recognise a further three, *viz*; the modification of the frontal sensory canal system (p. 140); the vertical LAP crest on hyomandibular and the longitudinally aligned *extensor tentaculi* muscle.

In addition to these basic silurid synapomorphies *Belodontichthys* possesses the following derived features with;

All Siluridae apart from *Silurus*:

1. Occipital canals elevated (p. 141)
2. Exoccipital contributes to cranial roof; vagus foramen relocated to posterior face (p. 141)
3. Dorsoanterior process of hyomandibular reduced or absent (p. 145; discussed in Bornbusch, 1988)

Exclusively with *Silurus, Wallago* and *Ompok*;

4. Raised lateral border of pterotic (p. 140)
5. Muscle A2 aligned vertically to jaw insertion (p. 149)
6. *Dilatator operculi* originating from the lateral ethmoid (p. 150)
7. Lateral parasphenoid shelf meeting similar pterosphenoid shelf (p. 140; see also Character 20)
8. Continuous row of long, recurved inner teeth in both jaws (p. 142)
9. Partially excavated frontals covered posteriorly with epaxial muscle (p. 139)

Exclusively with *Wallago* and *Ompok*;

10. Upwardly angled vomer and ethmoid (p. 139)
11. Thick, blunt ethmoid cornua (p. 138)
12. Reduced anterior fontanelle (p. 139)
13. Lateral branch of frontal sensory canal transversely or posteriorly directed (p. 140)
14. Expansion of ventral part of LAP hyomandibular crest (p. 145)

Exclusively with *Ompok*;

15. Parasphenoid angled upward relative to vertebral axis, its posterior part bearing a prominent keel (pp. 140)
16. Prominent frontal crests enclosing anterior and posterior fontanels (p. 139)
17. Raised border of pterotic (p. 140)
18. Reduced vomerine tooth patches, teeth supported on bony laminae or pedestels (p. 139)
19. Ventrally situated palatine articulatory facet on lateral ethmoid (p. 139)
20. Deep indentation of pterosphenoid–prootic junction and shelflike extension of optic nerve foramen (p. 140)
21. High and transversely aligned premaxillary ascending process (p. 143)
22. Helmet-shaped palatine (p. 147)

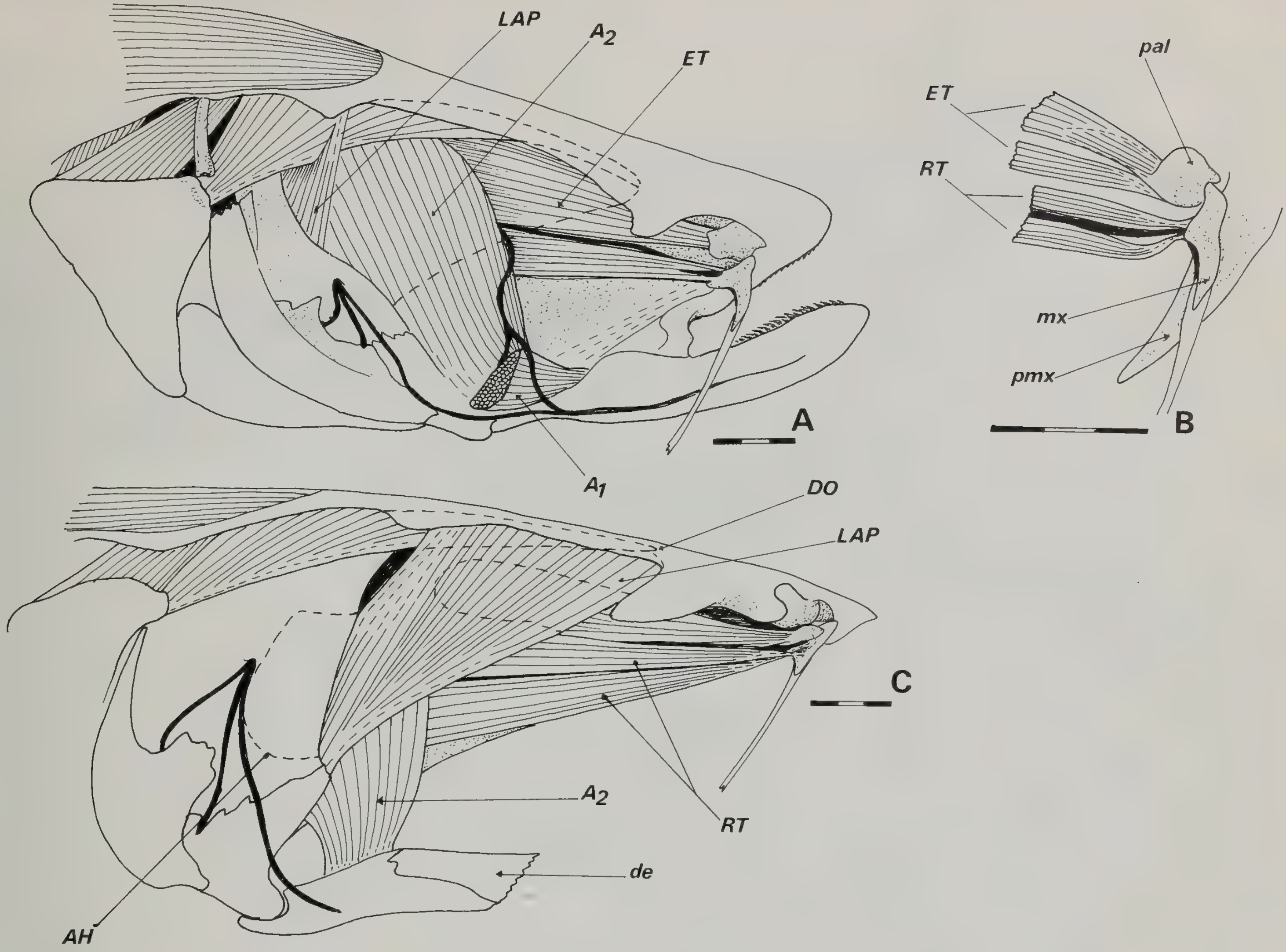

Fig. 21 A, *Silurus triostegus*: deep cranial musculature; most of muscles A1 and LAP removed; dashed lines indicate extent of DO and LAP; B, detail of insertion of ET and RT muscles (BMNH 1969.3.3:168–76); C, *Wallago attu*: deep cranial musculature; posterior border of the medial AH indicated by dashed lines on hyomandibular (BMNH 1891.11.30:156–61).

23. Dorsal margin of A1 portion of *adductor mandibulae* muscle contiguous with *epaxialis* musculature (p. 149)

Exclusively with *Kryptopterus bleekeri* and *K. apogon*;

Arrow-shaped tooth tips. This character has been discussed above (p. 143) and is interpreted as homoplastic in the light of its incongruent relative to the above listed synapomorphies.

Exclusively with *Kryptopterus* and *Hemisilurus* and some *Silurus* species;

Accessory foramen in prootic for hyomandibular branch of trigeminal nerve. This feature is difficult to evaluate as a synapomorphy linking these taxa with *Belodontichthys* since it occurs sporadically in *Silurus*. Its absence in other silurids must therefore be considered either as a derived loss or independently derived in *Belodontichthys*, some *Silurus* species, *Kryptopterus* and *Hemisilurus*; the latter situation being implied from the phylogenetic reconstruction given here (Fig. 27).

Phylogenetic interpretation

The distribution of these synapomorphies indicates *Belodontichthys* and *Ompok* as sister-taxa, forming the sister group to *Wallago* (Fig. 28). Ostensibly, through lacking three lower-level synapomorphies (Nos 1–3), *Silurus* is excluded from the main-body of Siluridae and appears as its sister-group. However, the six synapomorphies *Silurus* shares with *Wallago, Ompok* and *Belondontichthys* provide the more parsimonious system of relationships (Fig. 27).

The three less inclusive synapomorphies which *Silurus* lacks, namely, elevation of the semicircular canal tubes, repositioning of the vagus foramen and reduced anterodorsal process of the hyomandibular, may be viewed either as secondary loss and reacquisition or plesiomorphic retention. The first hypothesis demands that *Silurus* will have lost and regained one character (hyomandibular process) while retaining the plesiomorphic condition of the vagus foramen and semicircular canal (one loss and one gain). The other hypothesis demands that the two derived lineages would have independently acquired the vagus foramen and canal condition (two separate gains) whilst sharing the loss of the hyomandibular process with *Silurus*. In terms of losses and gains both hypotheses have equality.

In our view, we consider it anatomically more justified that *Silurus* has plesiomorphically retained these characters. In the positioning of the vagus foramen *Silurus* displays a transitional derived condition with respect to any non-silurid and the derived silurid lineages (it seems that this feature and the elevation of the semicircular canal tubes are functional correlates, the taxa with the largest vagus foramen, *Belodontichthys, Silurichthys* also have the tallest semicircular canal ridge). The anterodorsal process of the hyomandibular

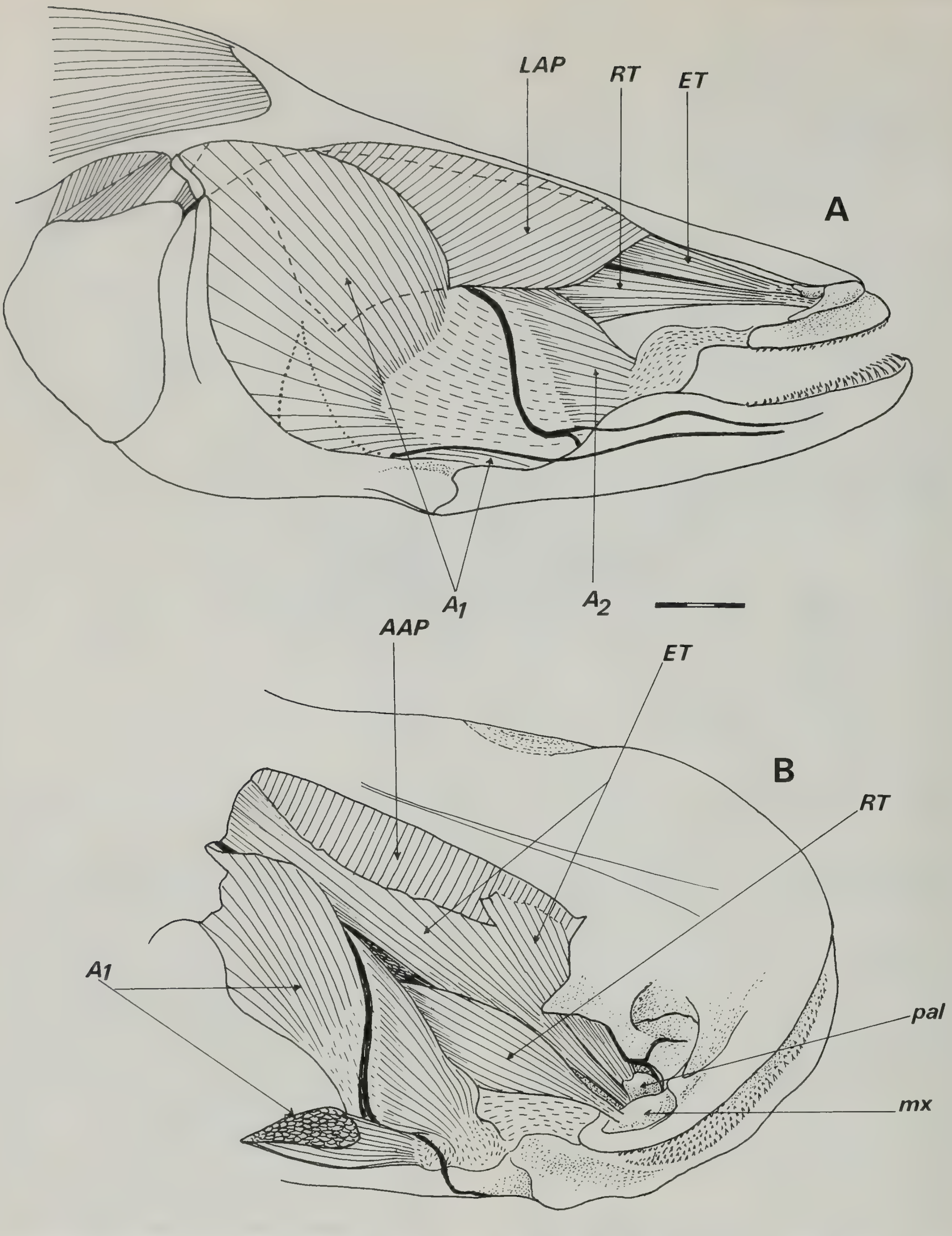

Fig. 22 *Kryptopterus bleekeri*: cranial musculature; A, lateral view with superficial part of A1 removed; dotted lines show course of hyomandibular nerves, dashed lines the outline of underlying LAP and DO muscles. B, dorsolateral view with LAP and DO muscle removed to show frontal attachment of AAP (LILI 89030).

is unlikely to have been lost and regained, since there would seem to be no functional reason to account for this pattern of events. Reasoning from an anatomical–functional viewpoint the vagus foramen-semicircular canal character should be the synapomorphy for the entire group minus *Silurus*. Identification of further synapomorphies from other anatomical complexes are needed to support one or other of these hypotheses. In this regard, Bornbusch (1988) has attempted a PAUP phylogenetic analysis involving several more characters utilized from the postcranial skeleton and has arrived at a conclusion different from ours. In his phylogeny, *Belodontichthys* appears as the sister group to one embracing *Kryptopterus apogon* group + *Ceratoglanis* and *Hemisilurus*; *Ompok bimaculatus* and *Wallago* are far removed from this group and *Silurus* appears as the sister-group to other Siluridae. The features by which Bornbusch relates *Belodontichthys* involve barbel length, barbel supports, truncated lateral process of the lateral ethmoid and short hyomandibular anterior process.

Our working concept of *Silurus* has been restricted to the type species *S. glanis* and *S. asotus*. Kobayakawa (1989) distinguishes two monophyletic groups of *Silurus* but the

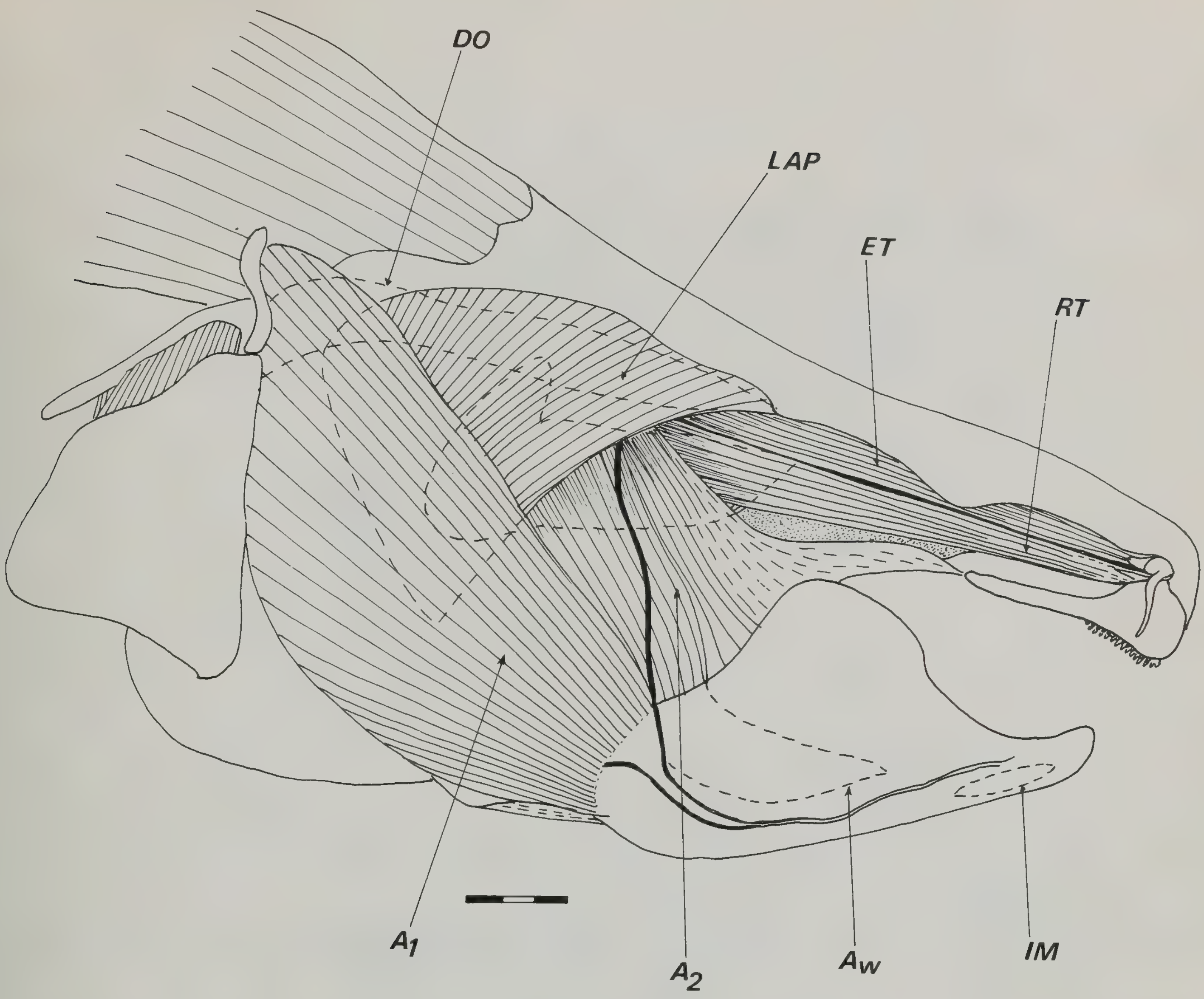

Fig. 23 *Hemisilurus heterorhynchus*: cranial musculature in lateral view; underlying AW, IM, Do, LAP and AAP muscles indicated by dashed lines (BMNH 1982.3.29:161–2).

synapomorphies she recognises as conferring monophyly on the genus appear insubstantial. Confluence of anal and caudal fins, reduced dorsal fin and rounded, truncated or emarginate caudal fin, the characters she proposes as synapomorphic for the genus, are not restricted to *Silurus* but occur elsewhere in the Siluridae and among other siluroids.

As recognised here *Ompok* includes, in addition to the type species, *O. bimaculatus, O. pabda,* and *O. liecanthus*. We have examined too few species to be sure of their generic assignment.

Our findings support those of Bornbusch (1988) that the genus *Kryptopterus* is non-monophyletic. Myological synapomorphies (orbital region of muscle A1 entirely tendinous; AAP and *retractor tentaculi* muscles extending from the medial surface of the frontal) appear to unite *K. bleekeri, K. apogon, K. cryptopterus* and *K. limpok*, species which Bornbusch (1988) grouped in two assemblages.

Hemisilurus, despite its specialized features (see Bornbusch & Lundberg, 1989) is myologically generalized and together with *Ceratoglanis* (Bornbusch & Lundberg, 1989) seems to be the sister-group to the other taxa considered. In our cladogram (Fig. 27) we have placed these and the other silurid genera (*Silurichthys* and *Hito*) together in a single unresolved lineage.

Neurocranial modifications and their evolution in *Belodontichthys*

The most outstanding feature of *Belodontichthys* compared with other Siluridae, and indeed other siluroids, is the excavation of the frontals and the occupation of the resultant space by epaxial muscle. The excavation has taken the form of a medial bowing giving a hull-like appearance to the skull roof. In addition to a change in profile, however, there has been a further modification to the anterolateral branch of the frontal sensory canal. This branch of the canal, itself a derived character of the Siluridae, is further derived in *Belodontichthys* by reversing direction to run posterolaterally (p. 140). The lateral opening of the canal retains its position above the orbit, anterior to the opening of the temporal canal with which it shares communication with the infraorbital canal. Thus, the lateral opening by virtue of its fixed position, presumably dictated early in the ontogeny of the sensory pore system, acts as a landmark from which to chart the topographical restructuring of the rest of the frontal and surrounding bones.

The posterior curvature of the lateral branch of the frontal canal is due to the anterior movement of the cross-commisure which is positionally associated with the posterior margin of

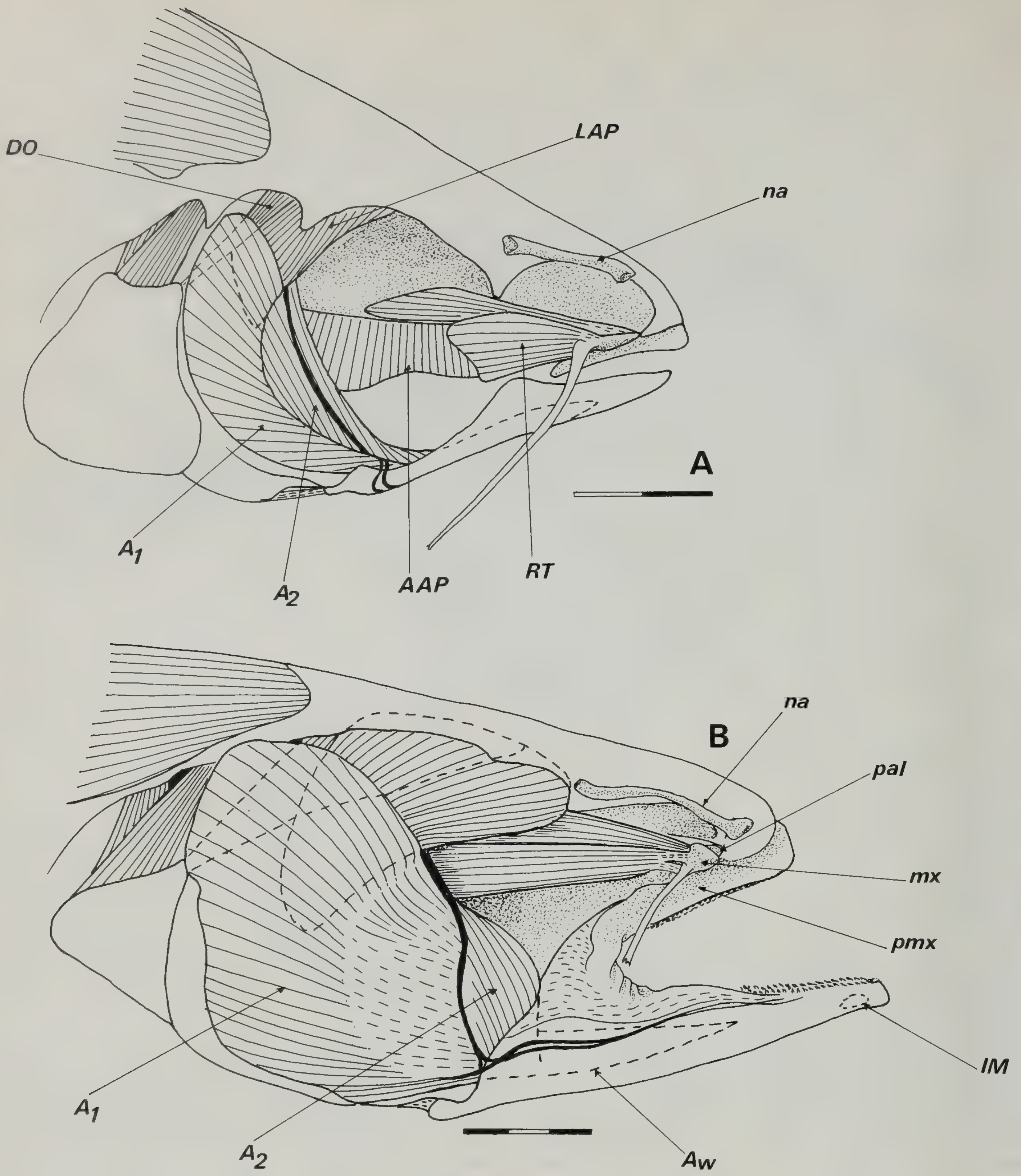

Fig. 24 A, *Kryptopterus bicirrhis* (BMNH 1982.3.29:163–7); B, *K. cryptopterus* (LILI 9009): cranial musculature in lateral view; underlying DO, LA, AW and IM muscles indicated by dashed lines.

the anterior fontanel. In *Belodontichthys* the anterior fontanel has become so shortened that it remains merely as a small opening between the frontal crests. The posterior fontanel is also reduced in size and almost obliterated by the medial crests.

The anterior relocation of the cross-commissure has given the impression of a shortened longitudinal sensory canal. However, although the anterior horizontal part of the canal is short in comparison to that in other siluroids, the remaining, posterior part of the canal has become vertically orientated owing to the medial elevation of the frontal to form a crest. When the length of the vertical part of the canal is taken into consideration it would seem that in overall length the longitudinal canal approximates that of other Siluridae.

The posterolateral branch of the frontal canal is possibly equivalent to the side branch noted by Lundberg (1982) which communicates with the infraorbital canal in most members of the Ictaluridae. In the Ictaluridae and Diplomystidae (Lundberg, 1982; Arratia, 1987), however, there is no link between the temporal canal of the sphenotic and the infraorbital canal, whereas in Siluridae there is a tripartite connection between the temporal, frontal and

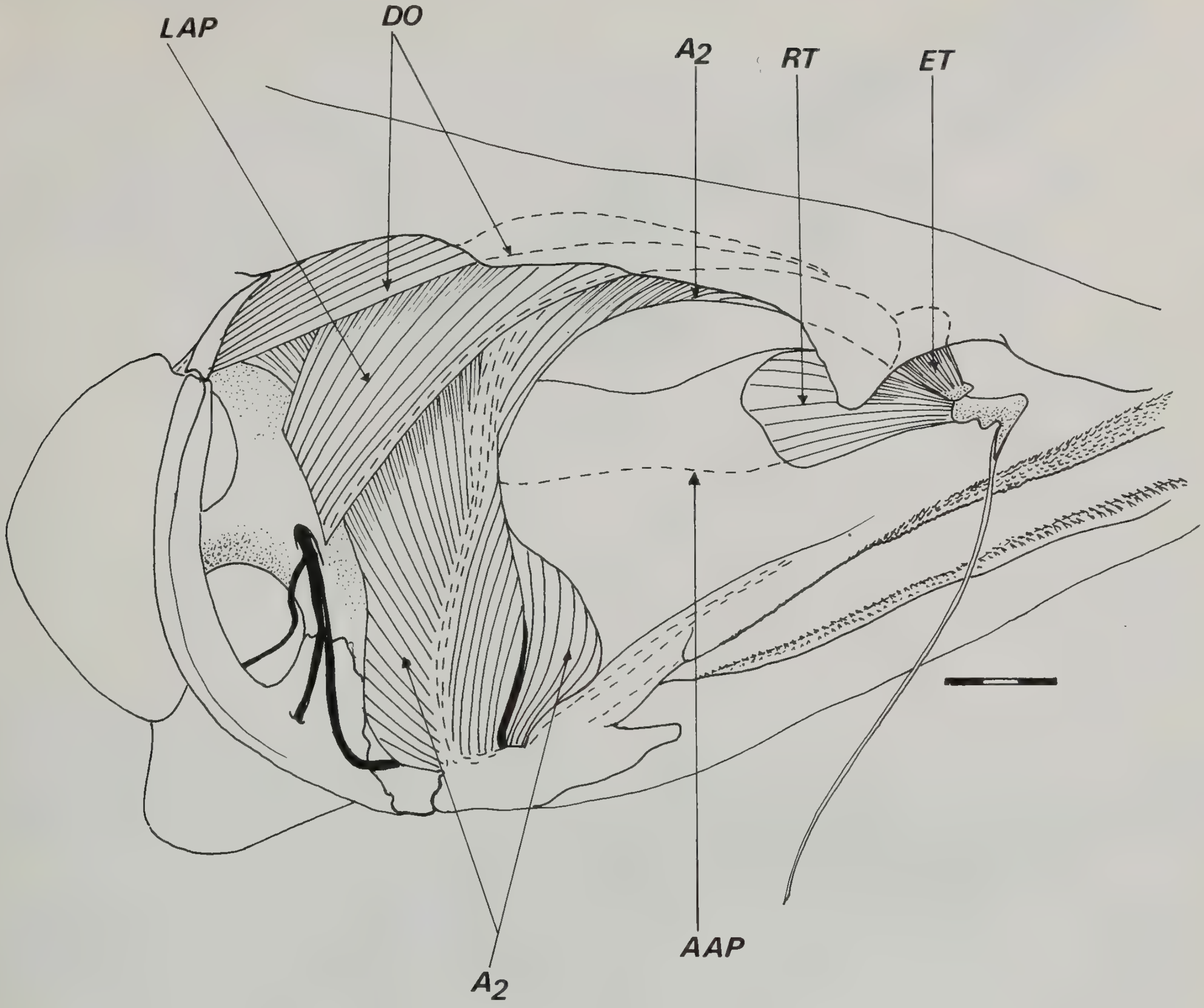

Fig. 25 *Eutropiichthys vacha*: deep cranial musculature; muscle A1 removed, underlying muscles shown by dashed lines. NB. AAP lies medial to pterygoid bones (BMNH 1891.11.30:162–9).

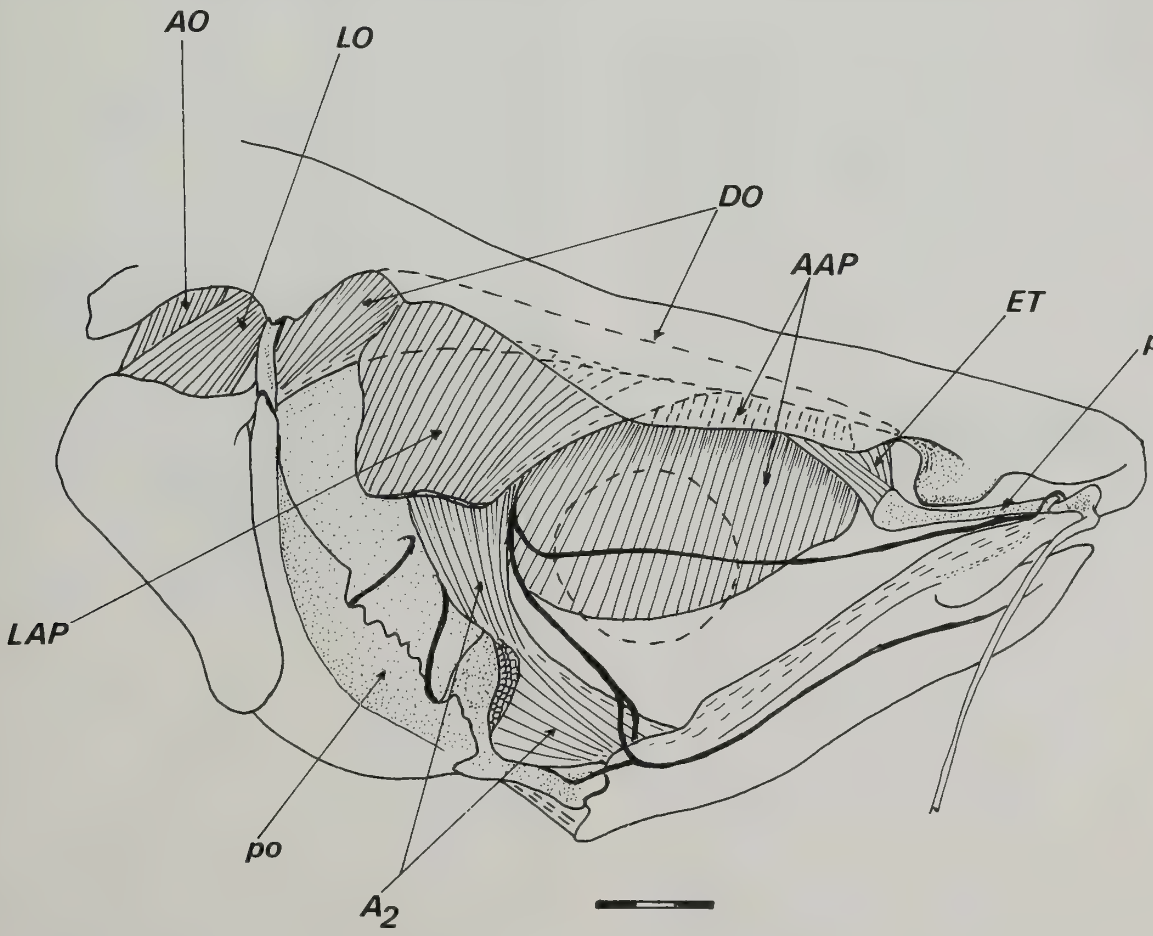

Fig. 26 *Schilbe mystus*: deep cranial musculature; muscle A1 totally, and A2 and LAP muscles partially removed; underlying muscles and position of eye indicated by dashed lines (BMNH 1982.4.13:3242).

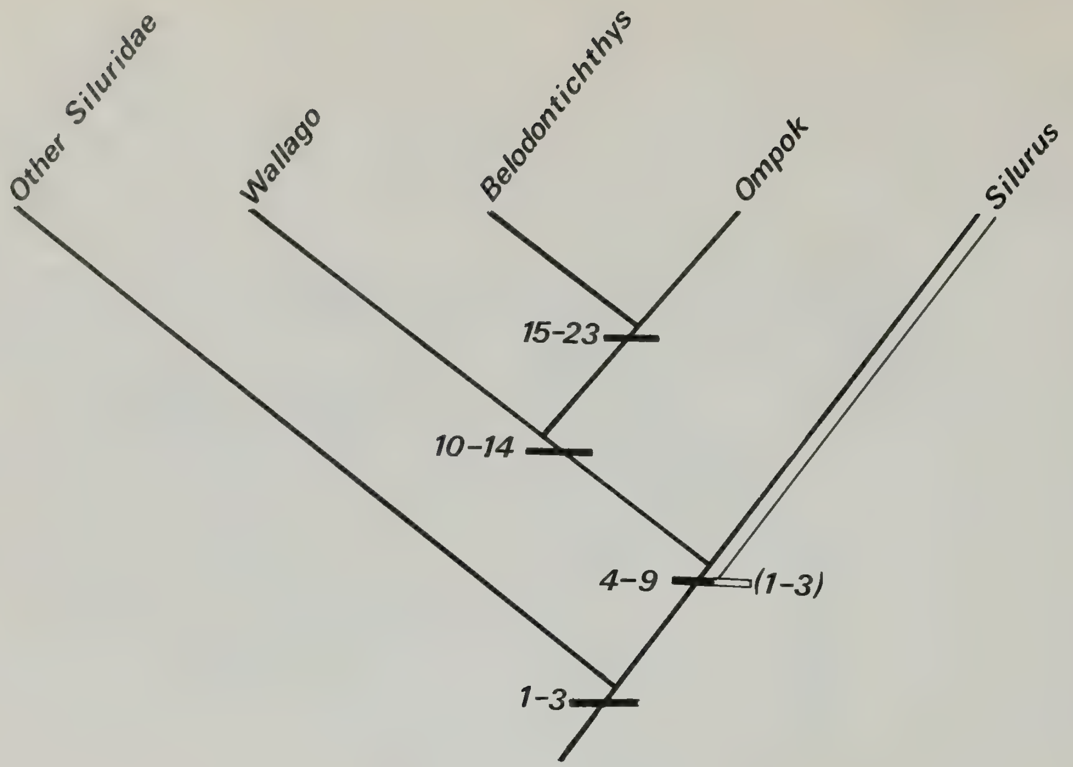

Fig. 27 Cladogram of Siluridae constructed from the synapomorphies discussed in the text (p. 00). Monophyly of the Siluridae follows Bornbusch (1990) with the addition of three other synapomorphies (1–3) involving frontal sensory canals, hyomandibular crest and *extensor tenatculi* muscle (p. 00). Characters 1–3 are absent in *Silurus* (see Discussion). The 'other Siluridae' lineage comprises *Hemisilurus, Ceratoglanis, Kryptopterus, Silurichthys* and *Ompok sensu lato* (see text).

infraorbital sensory canals. According to Lundberg (1982) the anterior displacement of the temporal canal branching point into the frontal is the result of jaw muscle insertion on to the cranium. In the Siluridae the development of the lateral branch of the frontal canal was also possibly initiated by encroachment of muscle onto the cranium, in this case, however, epaxial rather than jaw adductor muscle.

The sequence of phylogenetic changes culminating in the derived condition of the *Belodontichthys* cranium are evident in the successively derived sister-taxa *Wallago* and *Ompok* in which the lateral branch of the frontal sensory canal occurs transversely in the former and backwardly curved in the latter, with correlated anterior shifts of the cross-commissure, truncation of the anterior fontanel and posterior lengthening of the frontal crest. Concomitant with these changes in frontal topography is the forward encroachment with epaxial musculature on to the bone. In no other teleost known to us has the forward extension of the epaxial musculature produced such a profound modification to the frontals.

Among otophysans only two cyprinids *Macrochirichthys* and *Pelecus* display similar modifications. In both these taxa the frontals are concave but principally in the transverse and only slightly in the axial plane; in neither is there a median frontal crest. In both taxa the epaxial muscle extends to the anterior margin of the frontal, as in *Belodontichthys*. *Macrochirichthys* has anterior vertebral modifications which enable it to elevate the cranium, apparently to a considerable angle (Howes, 1979). Likewise, judging from the shape of the first centrum *Pelecus* may also have the ability to elevate the skull acutely. In the only other otophysans which have the capacity for marked cranial elevation (cynodontine characoids) the epaxialis musculature extends forward to the fronto-parietal ridge but the bulk of the muscle inserts into the posttemporal fossae (Howes, 1976). Cranial elevation in these fishes relies on the constriction of thick, longitudinal tendons fixed to the pterotic (Lesiuk & Lindsay, 1978). In these taxa and *Macrochirichthys* the epaxial musculature has a complex layering, with a lateral cage of intermuscular bones which prevents lateral distortion of the epaxialis when the head is flexed; furthermore, a highly-developed *supracarinales anterior* muscle is present (Howes, 1976; 1979).

None of these features is present in *Belodontichthys* and the firm attachment of the posttemporal to the pectoral girdle suggests that the forward extension of the epaxial musculature functions as a head-restraining rather than as a head-raising device. Bornbusch (1988) has pointed out that the posttemporal articulates with the 4th vertebral transverse process *via* a ball and socket joint which possibly allows cranial elevation. While we do not rule out the possibility of some degree of cranial elevation the firm union of the 1st centrum with the complex vertebrae suggest that the cranium is more or less fixed at an oblique angle, the degree of which is further enhanced by the even more acute upward angles of the parasphenoid and the ethmoverine block (p. 138). In this way a stable structure is formed against which the lower jaw can exert a powerful bite. In this respect the cranium of *Belodontichthys* more closely resembles that of the osteoglossomorph *Osteoglossum* (and to a lesser extent, *Scleropages*) which also has obliquely angled jaws and cranium, with an acutely angled parasphenoid, that promote powerful biting forces. In these fishes, however, the biting surfaces are principally between the toothed parasphenoid and basibranchial (Sanford & Lauder, 1990). Within siluroids, the closest functional equivalent appears to be the schilbeid, *Eutropiichthys vacha* which has paralleled the osteoglossoid 'tongue-bite' mechanism through the acquisition of extensively toothed vomerine and pterygoid toothed surfaces against which an inferior lower jaw bites. *Belodontichthys* lacks the vomerine and pterygoid development of *Eutropiichthys* and its lower jaw extends forward beyond the

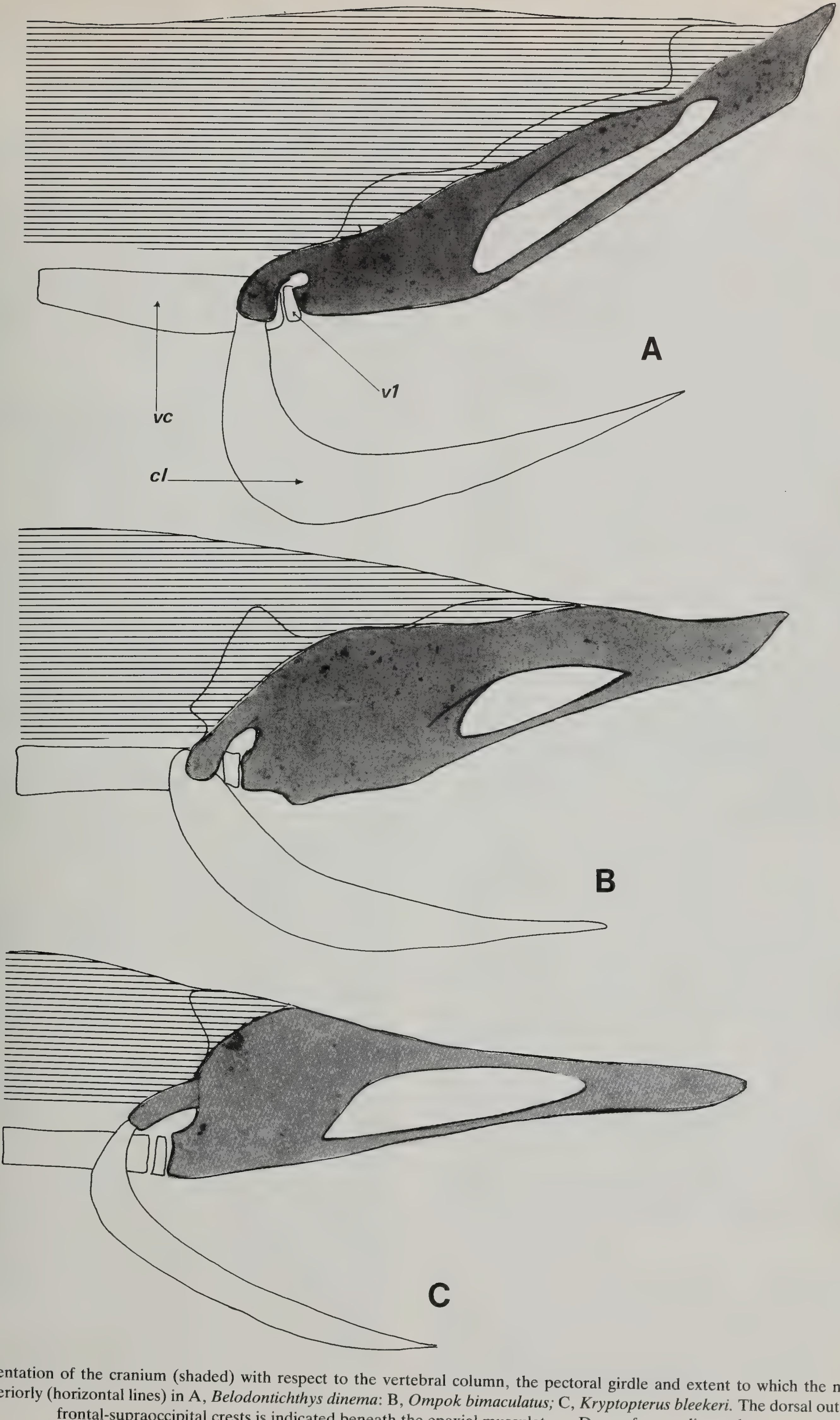

Fig. 28 Orientation of the cranium (shaded) with respect to the vertebral column, the pectoral girdle and extent to which the muscle has xtended anteriorly (horizontal lines) in A, *Belodontichthys dinema*: B, *Ompok bimaculatus;* C, *Kryptopterus bleekeri*. The dorsal outline of the frontal-supraoccipital crests is indicated beneath the epaxial musculature. Drawn from radiographs.

upper so that only the long inner row dentary teeth bite against the outer row of premaxillary teeth (Figs 1B, C).

The head and jaws of juvenile *Belodontichthys* appear much as in *Wallago* but during development the jaws become obliquely aligned (C. Vidthayanon pers. comm.). Whether the epaxial muscle continues to extend forward onto the cranium during early development is unknown.

A low coronoid process of the lower jaw is a feature common to all those teleosts with long jaws having a snapping action, as are long caniniform teeth arranged in single or double rows. The latter feature is rare in siluroids, where the characteristic dentition is short, multi-rowed, villiform teeth. The only other siluroid to have a single row of large caniniform teeth is the sisorid, *Bagarius*, a large predatory fish with a widespread distribution in India and south east Asia (Roberts, 1983).

Belodontichthys falls into the category of teleosts which Ganguly & Chatterjee (1963) referred to as 'bilaterally compressed snapping teleosts' and in which they included *Ompok* and *Eutropiichthys*. *Belodontichthys* displays a morphotype which at first sight one might label as typically that of a 'neck-bending' teleost but closer examination reveals that this 'typical' morphology in fact characterises the converse functional situation, namely one providing a rigid rather than a flexible framework, presumably allowing more powerful biting forces.

We believe that the specialized features of the *Belodontichthys* cranium have arisen as a result of coordinated factors comprising cranial re-alignment with respect to the vertebral axis and the encroachment of epaxial muscle onto its surface (Fig. 28). The epaxial muscle encroachment has also resulted in the differential growth of the central areas of the frontal relative to its lateral areas thus maintaining the fixed position of the sensory canal pores around the perimeter of the muscle bloc. The jaw teeth have elongated and the dentigerous area has been reduced but the characteristic silurid prognathous lower jaw has been retained.

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A collection of sea snakes from Thailand with new records of *Hydrophis belcheri* (Gray)

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SYNOPSIS. A report is given on a collection of sea snakes made, between 1979–1986, by fishermen at various localities around the coasts of Thailand. The commonest species, at many sites, were *Lapemis hardwickii* and *Hydrophis cyanocinctus*.

A poorly known sea snake, *Hydrophis belcheri*, is recorded from Thailand for the first time and the larger sample size allows for variation in the meristic characters of this species to be better assessed. Another new record for Thailand is *Hydrophis fasciatus fasciatus* however the occurrence of this subspecies on the west coast has long been anticipated.

One specimen (*Hydrophis* sp.) proved especially difficult to identify, it is provisionally regarded as being close to *H. lapemoides*.

Some common Thai species, such as *Hydrophis brooki* and *H. torquatus* were not collected; the possible reasons for these intriguing absences are discussed.

INTRODUCTION

The waters of Thailand have an extremely diverse sea snake fauna being adjacent to areas traditionally regarded as a "centre of distribution" of the group (Voris, 1977; Vitt, 1987: 347). The west coast of Thailand is close to the Straits of Malacca (where at least 27 species of sea snake are known to co-exist) and the east coast borders the Gulf of Siam (from where around 16 species have been recorded). The region, by virtue of its central position, is particularly prone to new range extension records for sea snakes (e.g. Frith, 1977; Rasmussen, 1987). However, problems of identification are inclined to cloud the picture when it comes to drawing-up a faunal list for the area, particularly in relation to the difficult genus *Hydrophis* e.g. Suvatti (1950) recorded a surprisingly large number of species but as Tu (1974): 207) observed, 'the names used by Suvatti may not be accurate'.

In an extensive investigation in the Gulf of Thailand (Tu, 1974) where 14 282 sea snakes were collected, *Lapemis hardwickii* was found to be by far the most common species (accounting for some 81% of the sea snakes caught). Among the remaining species there were clearly some problems with identification (3.4% of the specimens were not identified) and Tu (1974: 203) commented that most of the unidentified snakes belonged to the genus *Hydrophis*. Recently Steubing & Voris (1990) noted marked similarities between marine snake collections made in the Gulf of Thailand and those from the coast of Sabah, Malaysia.

MATERIALS AND METHODS

Between the years 1979 and 1986 one of us (D.W.) was resident in Thailand, and requested fishermen from various settlements around the Gulf and along the west coast to preserve any sea snakes that they encountered in the course of their fishing trips. Unfortunately, this meant that precise locality data are lacking, but as the pattern of fishing dictated that boats left and returned to port on the same day the distances covered were never great. Two hundred and eighty-eight specimens in all were obtained; the material is preserved in the British Museum (Natural History). A list of species is given in Table 1 and the Appendix.

By far the commonest species, found at many of the

Table 1. Sea snakes recorded from Thailand

Laticauda colubrina	1, 2, 5, 7a
L. laticaudata	1, 2, 4, 5?, 8c
L. semifasciata	4
Aipysurus eydouxii	1, 2, 3, 5, 6, 9
Emydocephalus ijimae	4
Acalyptophis peronii	2, 5, 6
Astrotia stokesi	2, 4, 5
Enhydrina schistosa	1, 2, 3, 4, 5, 6, 9
Hydrophis belcheri	9
Hydrophis brookii	1, 2, 3, 5, 6
H. caerulescens	1, 2, 3, 5, 9
H. cyanocinctus	1, 2, 3, 4, 5, 6, 9
H. elegans	5
H. fasciatus	1, 2, 5, 9
H. f. atriceps	1, 3, 9
H. gracilis	1, 4, 5, 6
H. g. microcephalus	1
H. klossi	1, 2, 3, 5, 6, 9
H. lamberti	1, 8b, 9
H. lapemoides	8a, 9
H. mamillaris	1, 5?
H. melanocephalus	4
H. nigrocinctus	1
H. ornatus	1, 2, 3, 4, 5, 6, 9
H. spiralis	4, 5?, 7b, 9
H. torquatus	2
H. t. aagaardii	1
H. t. diadema	1, 2, 3, 6
H. sp. (?nr. *lapemoides*)	9
Kerilia jerdonii	1, 2, 3, 4, 5
K. j. siamensis	1, 2, 6
Kolpophis annandalei	1, 2, 5
Lapemis hardwickii	1, 2, 3, 4, 5, 6, 9
Lapemis curtus	4
Pelamis platurus	1, 2, 3, 4, 5, 6, 9
Praescutata viperina	1, 2, 3, 4, 5, 6, 8c, 9
Thalassophis anomalus	1?, 3, 6

1. Suvatti (1950)
2. Taylor (1965)
3. Barme (1968)
4. Tu & Tu (1970)
5. U.S. Navy (1965)
6. Tu (1974)
7(a) Frith (1974 (b) Frith (1977)
8(a) Rasmussen (1987) (b) Rasmussen (1989*a*) (c) Rasmussen (1989*b*).
9. Present collection (Warrell, this paper)

localities, was *Lapemis hardwickii* (accounted for over 42% of the sea snakes preserved). Next most common was *Hydrophis cyanocinctus* (27% of the catch). A most notable feature is the presence of *Hydrophis belcheri*; apparently this constitutes the first record of this species from Thai waters.

SYSTEMATIC ACCOUNT

This account deals only with the most noteworthy species in the collections.

Hydrophis belcheri (Gray, 1849)

INTRODUCTION. The name *Hydrophis belcheri* has had a rather confused history leading to a redefinition by McDowell (1972). Confusion stems partly from the influential work of Smith (1926) whose concept of *H. belcheri* is now recognised as being too broad. In fact *H. belcheri* (sensu Smith) is apparently a composite of at least four species:
(1) *H. belcheri* (sens. strict.) which is discussed below.
(2) *H. (Leioselasma) melanocephalus* a species recognised by Smith but thought by him to be restricted 'to the Riu Kius and the coast of Formosa'.
(3) *H. (Leioselasma) pacificus* regarded as a synonym of *belcheri* by Smith but recognised as distinct by Cogger (1975).
(4) *H. (Leioselasma) coggeri* which Kharin (1984) described to accommodate Australian examples that had previously been assigned to *melanocephalus* by McDowell (1972) and Cogger (1975). This is probably the correct name of the 'most venomous snake' cited in McFarlan 1989 (*The Guinness Book of Records 1990*) as '*Hydrophis belcheri*'. The Guinness Book does not provide a reference, but it is almost certainly based on the work of Tamiya & Puffer (1974), who described the lethality of several sea snake venoms including '*H. belcheri* from Ashmore Reef', the most toxic of all. However, Tamiya (1975) and Cogger (1975) equivocally regarded Ashmore Reef *belcheri* as *melanocephalus* indicating that its taxonomic status was still under review.

In its strict sense, *H. belcheri* is apparently known only from a few individuals. The type of *H. belcheri* is allegedly from New Guinea, while McDowell (1972) records another example from the Java Sea; two further specimens were collected during a fisheries survey of the Java Sea in 1976 and are now preserved in British Museum (Natural History). Apparently, nothing further has been recorded, to add to the known range of *H. belcheri*, which makes the occurrence of 14 specimens, reported here, from various localities in the Gulf of Thailand, all the more remarkable. Such a significant increase in the available sample of *H. belcheri* makes it worthwhile re-examining the diagnostic characteristics of the species and evaluating the variation found.

MATERIAL (Fig. 1). Holotype: BMNH 1946.1.1.97 (formerly 42.11.22.30) 'New Guinea'. Java Sea: AMNH 63947 off Karima Djava Island (reported by McDowell 1972). BMNH 1977.125 Off S. Coast of Kalimantan. BMNH 1977.126 06°28′ S: 110°30′ E

Gulf of Thailand: BMNH 1987.42–49 Tachalab, near Chanthaburi; BMNH 1987.50–53 Samut Sakhon; BMNH 1987.54 Pattani; BMNH 1987.55 Nakon Si Thammarat.

DESCRIPTION. **Scalation:** Scale rows on neck 24–26, scale rows at midbody 32–36. Body scales are imbricate and somewhat variable in shape, some are hexagonal others (particularly on the posterior part of the body) are more rounded. Ventrals are more than twice as broad as adjacent costals and range in numbers from 278 to 313. There are 28 to 42 subcaudals. Supralabials usually seven (rarely six or eight) normally only a single supralabial (the fourth) borders the eye but, rarely, two border the eye (third and fourth or fourth and fifth). Infralabials eight or nine (rarely ten), no cuneate scales. Preoculars one, postoculars normally two (occasionally one or three), anterior temporals usually two (sometimes one).

Coloration: Head usually black with flecks of olive and, fairly frequently, at least traces of a yellowish horse-shoe shaped mark on prefrontals and around eye. Body with 48–64 dark bands that are broad dorsally but narrow on the flanks; tail with 4–8 dark bands.

Size: Largest male, total length, 855 mm; tail 82mm.
Largest female, total length, 932 mm; tail 75 mm.

Dentition: Maxillary teeth II + 7 (sometimes II + 8, rarely

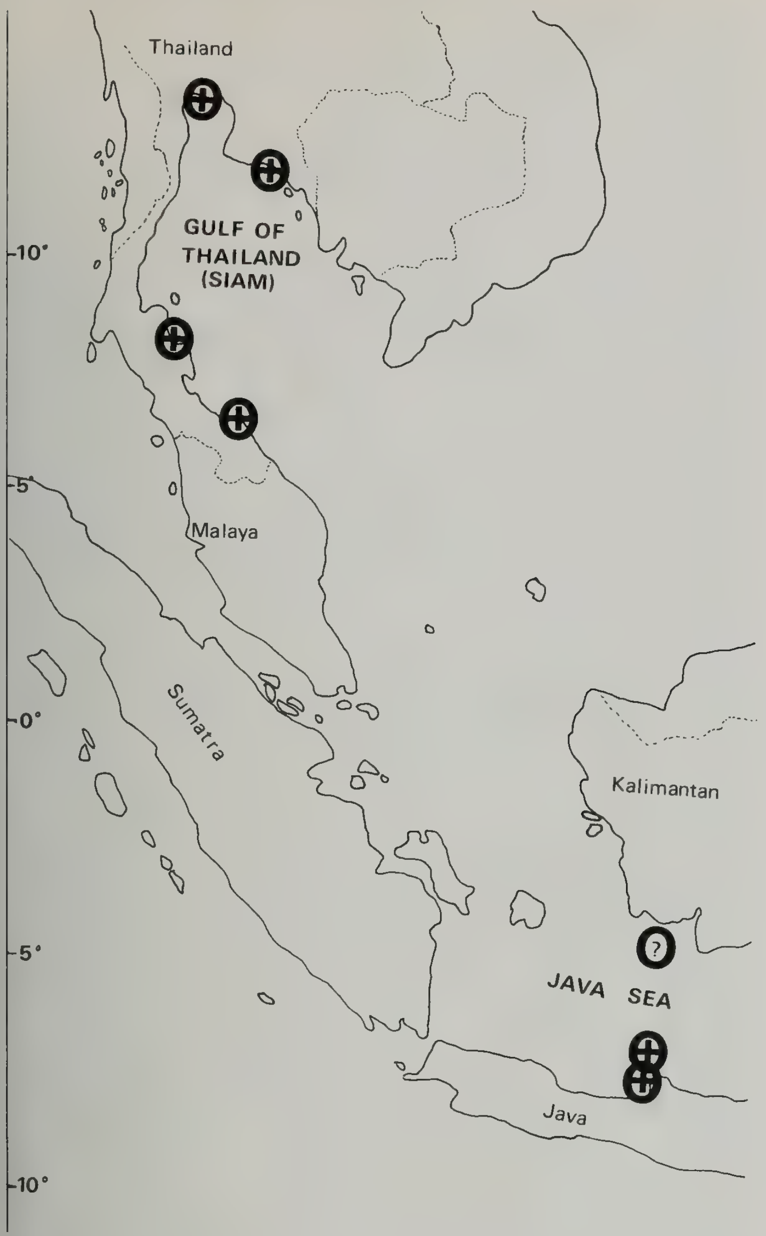

Fig. 1 Distribution of *Hydrophis belcheri*. + = Precise localities; ? = An imprecise locality 'Off S. of Kalimantan'; the holotype is alleged to have come from 'New Guinea', but this vague locality is regarded as dubious, no other examples appear to have been collected in the vicinity.

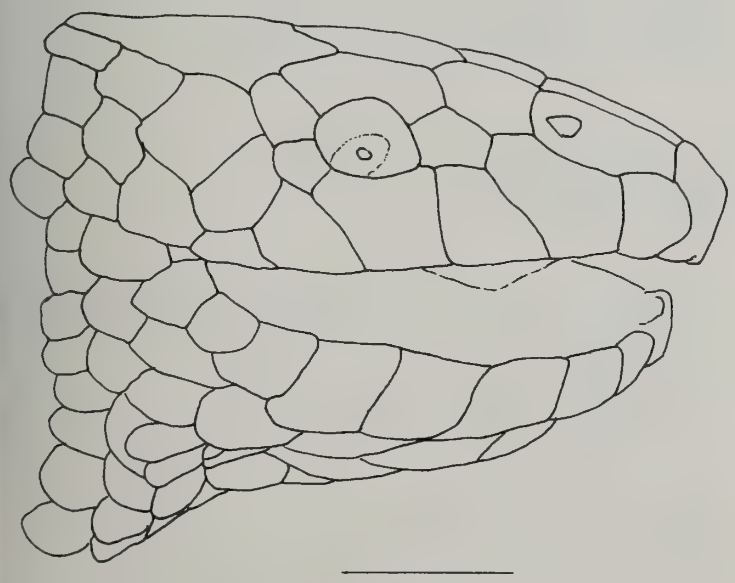

Fig. 2 Lateral view of the head of *Hydrophis belcheri* (BMNH 1987.48). Note only a single supralabial (the fourth) contacts the eye. (Scale = 5 mm).

II + 6 or II + 9); palatine teeth 7–9; pterygoid teeth 14–17; dentary teeth 17–19.

Additional features: Sphenoid entering broadly into the ventral margin of the cavum epiptericum. Snout falls two to three tail lengths short of the cloaca when body doubled at heart.

Relationships: Assigned by McDowell (1972) to subgenus *Aturia*. Within this subgenus there appear to be two groups of species: *torquatus* et al. and *ornatus* et al., McDowell (1972: 226) regards *belcheri* as being 'intermediate between these two groups'.

DIAGNOSIS. *H. belcheri* may be diagnosed on the basis of the combination of features mentioned above. One of the most reliable characters is the possession of a single supralabial contacting the eye, Fig. 2, (apparently unique among *Hydrophis* sens. lat.). However some variation is noted here for the first time: One male (BMNH 1987.51) showed assymetry, on the right side of the head there is the characteristic condition of a single supralabial (the fourth) entering the eye while, on the left, two supralabials enter the eye (the third and fourth). The other exception is a female, BMNH 1987.42, which has two supralabials entering the eye on both sides. This female contained four young (BMNH 1987.43–46) three of which have apparently inherited the atypical condition of multiple supralabials entering the eye while the remaining specimen (BMNH 1987.46) has only the fourth doing so. McDowell (1972) assigned *belcheri* to subgenus *Aturia* which may be distinguished from subgenus *Hydrophis* by its lack of a triangular flange on the palatine and from subgenus *Leioselasma* by sphenoid entering broadly into the anterior oriface of the cavum epiptericum. Within the *Aturia* key presented by McDowell (1972: 228–229) *belcheri* is grouped with those species that have the heart just behind the anterior third of the body (i.e. with *lapemoides, bituberculatus, ornatus,* and *inornatus*).

Distinguished from *lapemoides* by the absence of cuneate scales on the lower lip and generally fewer maxillary teeth (usually 7 in *belcheri* vs. 8–11 in *lapemoides*). *H. ornatus* and *inornatus* similarly have more maxillary teeth (10–13). *H. bituberculatus* appears closest to *belcheri* but has strongly keeled scales (almost smooth in *belcheri*).

Hydrophis lapemoides (Gray, 1849) and ***Hydrophis*** sp.

H. lapemoides was long considered to be predominantly a Persian Gulf species, although ranging as far east as India and Sri Lanka (Smith, 1926; Minton, 1966; Ahmed, 1975). Recently however, *lapemoides* has also been collected in Malaysia: Penang (Toriba & Sawai, 1981) and the southern part of the Straits of Malacca (Rasmussen, 1987), and on west coast Thailand: Phuket Island (Rasmussen, 1987) and Krabi (BMNH 1987:1166, present collection). The status of specimens, identified as *lapemoides,* from the Philippines (Tamiya, Maeda & Cogger, 1983) was questioned by Rasmussen (1987) who had no authentic records of *lapemoides* east of the Straits of Malacca.

Therefore the occurrence of a problematic specimen, which appears closest to *lapemoides,* from the Gulf of Thailand (Samut Sakhon, BMNH 1987.172 present collection) is of some interest. Arne Rasmussen (in litt.) kindly compared the Samut Sakhon specimen with material of *lapemoides, lamberti, inornatus* and *ornatus,* and it appears that the specimen is closest to *H. lapemoides*.

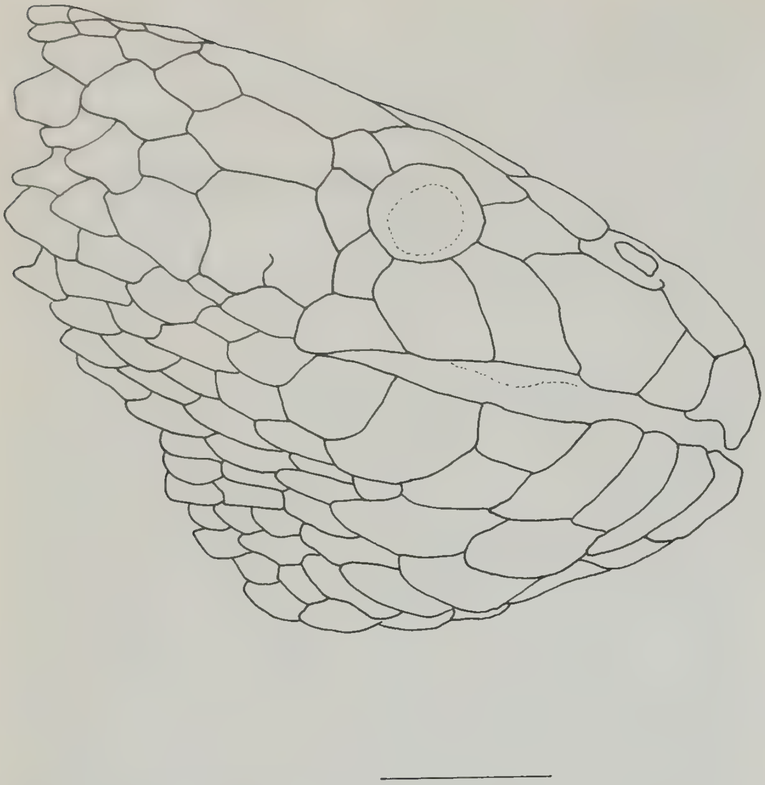

Fig. 3 Lateral view of the head of *Hydrophis* sp. (near *lapemoides*) BMNH 1987.172. (Scale = 5 mm).

This specimen will be more fully assessed in a future review of questionable '*lapemoides*' specimens (Rasmussen, pers. comm.) in the mean time it is referred to as *Hydrophis* sp. (near *lapemoides*).

Hydrophis fasciatus (Schneider, 1799)

Hydrophis fasciatus is widespread from India to China and New Guinea. Two races are recognised, the region of Singapore seemingly marking the boundary between them; *H. f. fasciatus* occurring to the west of Singapore and *H. f. atriceps* to the east. The nominate form, according to Smith (1926), has more elevated scale counts (48–58 at midbody, 414–514 ventrals) compared with *atriceps* (39–49 at midbody, 323–453 ventrals). It appears that only *H. f. atriceps* has previously been collected in Thai waters and indeed, in the present collection, this was the commoner form. Twenty-five *H. f. atriceps* were obtained from localities bordering the Gulf of Thailand (BMNH 1987.143, 145, 147–149 Nakon Si Thammarat; BMNH 1987.150–154 Chumporn; BMNH 1987. 155–163, 165, 167–171 Tachalab near Chanthaburi). However, as Taylor (1965: 1047) observed, 'little collecting has been done on the coast of the Bay of Bengal and *H. f. fasciatus* may be found there'; this hypothesis has been confirmed by five specimens in the present collection from Kantang, near Trang, West Coast Thailand (BMNH 1987. 138–142), this seems to be the first record of the nominate form from Thailand.

DISCUSSION

As previously mentioned, perhaps the most notable aspect of the present collection is the presence of *Hydrophis belcheri*; a species not previously recorded from Thailand. Another surprising feature is the absence of some species that have previously been reported as common in Thai waters. Neither *H. brookii* nor *H. torquatus* were found, whereas Taylor (1965) reported both as being common in the Gulf of Thailand. Some reasons that might account for this anomaly could include the strictly local nature of the abundance in some forms, or perhaps seasonal fluctuations and migrations of some species. Evidence from the literature is unfortunately thin; there is some suggestion that sea snakes sometimes do seasonally fluctuate in numbers. Tu (1970), for instance, found that *Enhydrina schistosa* is most abundant in estuaries during the dry season (December to April); this is accounted for by the snakes migrating up river mouths during this period, when the tidal influx of sea water is at its greatest. Regrettably little is known regarding the factors affecting the distribution of *H. brookii* or *H. torquatus*. Taylor (1965: 1052) merely noted that *H. brookii* 'is common in the Gulf of Siam, especially so at Songkhla, where a series of 42 were taken, it is known also on the western side of Thailand on the coast of Trang Province'. Regarding *H. torquatus* subspp., Taylor (1965) noted that *H. t. diadema* 'is particularly abundant at the mouths of the Meklong and Chanthaburi rivers', whereas *H. t. aagardi* according to Smith (1920) occurs in 'deep clear sea water, as far as 20 miles from the coast', and Taylor's (1965) series was 'taken largely in the Sea of Singgora'.

In figures given by Tu (1974: 202) for collections in the Gulf of Thailand for the years 1967, 1969 and 1972 there are apparent fluctuations in the incidence of *H. torquatus diadema*, i.e. none were recognised among collections of 355 and 5311 sea snakes in 1967 and 1969 respectively, but 250 were in a collection of 6970 sea snakes in 1972. However, one factor making this difficult to evaluate is the significant number of 'unidentified' specimens (50 in 1967, 165 in 1969), Tu indicates that some *H. torquatus diadema* were 'probably included in the unidentified category' in 1967 and 1969. Similarly, *H. brookii* was not recorded during the 1967, 1969 or 1972 investigations, but was subsequently found among unidentified material, so that too was almost certainly underestimated.

While intriguing, there are a great many possibilities to account for the absence of apparently common species in the present collection, and without more information regarding conditions forming the background to success or failure of capture it is difficult to address the problem.

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APPENDIX

Material in present collection (listed by location)

Locality	Identification	Numbers
Gulf of Thailand		
Sai Buri	*Aipysurus eydouxii*	1
	Hydrophis cyanocinctus	1
	Lapemis hardwickii	13
	Praescutata viperina	5
Tachalab, nr. Chanthaburi	*Aipysurus eydouxii*	4
	Hydrophis belcheri	8
	H. caerulescens	8
	H. cyanocinctus	35
	H. fasciatus atriceps	14
	H. klossi	4
	H. ornatus	1
	Lapemis hardwickii	30
Samut Sakhon	*Hydrophis belcheri*	4
	H. cyanocinctus	10
	H. lamberti	4
	H. ornatus	3
	H. sp. (nr. *lapemoides*)	1
	Lapemis hardwickii	1
Pattani	*Hydrophis belcheri*	1
Nakhon Si Thammarat	*Hydrophis belcheri*	1
	H. caerulescens	2
	H. cyanocinctus	20
	H. fasciatus atriceps	5
	H. ornatus	1
	Lapemis hardwickii	11
Chumphon	*Hydrophis cyanocinctus*	5
	H. fasciatus atriceps	5
	Lapemis hardwickii	54
Wang Gaew	*Pelamis platurus*	1
Chon Buri	*Pelamis platurus*	1
West Coast		
Satun	*Enhydrina schistosa*	1
Kantang, nr. Trang	*Hydrophis cyanocinctus*	5
	H. f. fasciatus	5
	H. klossi	1
	H. spiralis	4
	Lapemis hardwickii	8
Phuket Island	*Hydrophis ornatus*	1
	Lapemis hardwickii	15
Krabi	*Hydrophis cyanocinctus*	2
	H. lapemoides	1

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The copepod inhabitants of sponges and algae from Hong Kong

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SYNOPSIS. Eight new siphonostome species, including two of new asterocherid genera were found in sponges and algal washings collected in Hong Kong. These are described.

INTRODUCTION

Little work has been done on the taxonomy of the benthic copepods of Hong Kong, with the exception of Boxshall (1990) who described some sponge-dwelling siphonostomes from the present collection series. It is insufficient, however, to state that an area requires study simply because it has been neglected. Hong Kong copepod fauna is compelling not only because it is poorly known, but also because it is diverse. Siphonostomes are found in all sorts of invertebrate hosts. Schirl (1973) reviewed the associates of a number of hosttypes. Huys (1990) reported over 80 copepod species in sponges alone, to these must be added Boxshall's new siphonostomes and those described here.

MATERIALS AND METHODS

The material was collected by divers in shallow waters at various stations around the coast of Hong Kong during the Second International Workshop on Marine Flora and Fauna of Hong Kong and Southern China. Station localities are given in the descriptions. The collections were made in April 1986. The sponges and algal fragments were preserved in 4% sea-water formalin. The sponge hosts have yet to be identified, samples of each are available for examination at the Natural History Museum, London.

Dissections were made with lactophenol and chlorazol black, permanent mounts were made in polyvinyl lactophenol. In the descriptions, spines are given in roman numerals and setae in arabic numerals. Body length measurements were taken from the rostral tip to the distal margin of the caudal rami; body segments were measured along the dorsal midline, and the first antenna along the non-setose inner margin. Proportional lengths of urosome segments include the caudal rami. The material is stored at the Natural History Museum in London.

Family DINOPONTIIDAE Murnane

Stenopontius boxshalli n. sp.

Figs 1–3C

MATERIAL EXAMINED. Holotype ♀, allotype, 2 ♂♂ paratypes from the sponge *Ricinia* sp. collected at a depth of 15m at Chik Chau on 6 April 1986. BM(NH) registration numbers 1989.193 (holotype), 1989.194 (allotype), 1989.195 and 196.

ETYMOLOGY. This species is named after Dr Geoffrey Boxshall in recognition of his work on the taxonomy and anatomy of copepods.

FEMALE. Elongate, dorso-ventrally flattened, ornamented with rows of spinules, 0.52mm long. Relative lengths of urosome segments 6: 33: 14: 15: 15: 17. Genital segment 0.7 times as long as wide, apertures dorso-laterally placed at midpoint, segment widest here, but not much swollen (Fig. 1). Egg sacs paired, each sac with 2 eggs. Anal segment 0.7 times as long as wide. Genital and third urosome segment ornamented with rows of spinules on posterior margins. Caudal rami 2.5 times as long as wide, roughly cylindrical, with 4 terminal, 1 lateral and 1 dorsal setae of varying lengths.

First antenna 14-segmented (Fig. 2A); relative lengths 18: 5: 5: 3: 1: 4: 7: 16: 6: 9: 4: 6: 6: 10; armature I–0; II–0; III–2; IV–1; V–1; VI–3; VII–3; VIII–1; IX–0; X–1; XI–1; XII–1; XIII–2; XIV–4. Second antenna with terminal claw, otherwise unarmed, also lacking exopodite (Fig. 2B). Siphon very short and squat (Fig. 2C). Mandible represented by stylet. Outer lobe of first maxilla with 2 terminal setae; inner lobe larger with 3 terminal setae (Fig. 2D). Terminal segment of second maxilla produced with claw, tip with row of spinules (Fig. 2E). Maxilliped 3-segmented, robust and with terminal claw (Fig. 2F).

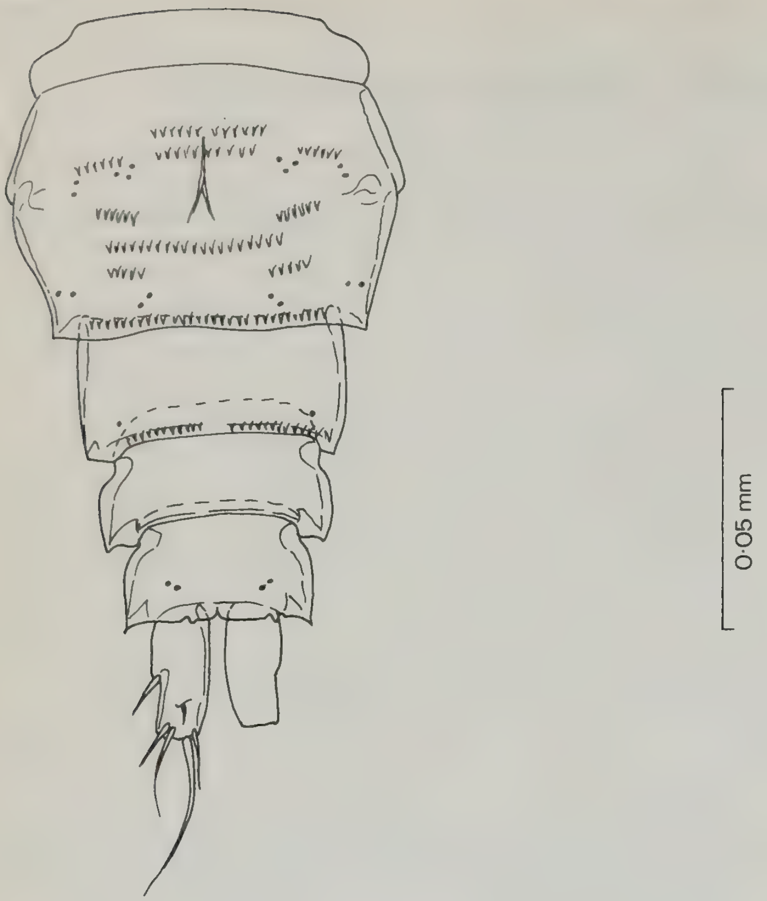


Fig. 1 *Stenopontius boxshalli* n. sp. ♀, holotype. Urosome, dorsal view.

Armature of natatory legs (Fig. 2G–J):

	Coxa	Basis	Endopodite	Exopodite
Leg 1	0–0	0–I	0–1; 0–1; 1,1,4	I–0; I–1; II, 2,2
Leg 2	0–0	0–0	0–1; 0–2; 1,2,3	I–1; I–1; III, I,5
Leg 3	0–0	0–0	0–1; 0–2; 1,1,3	I–1; I–1; III, I,5
Leg 4	0–0	0–0	0–1; 0–2; 0,2,2	I–1; I–1; III, I,5

External margins of segments spinulose. Fifth leg 2-segmented and leaf-like, terminal segment twice as long as wide with 2 terminal spines and 1 seta (Fig. 2K).

MALE. Body shape and ornamentation as for female, 0.48, 0.50 and 0.52mm long (Fig. 3A). Prosome equal in length to urosome, of uniform width in posterior half; head equal in length and width, rostrum not visible; relative lengths of prosome segments 49: 20: 17: 14; relative lengths of urosome segments 7: 32: 11: 14: 11: 11: 14. Genital segment 0.7 times as long as wide, all urosome segments with winged posterior margins and postero-ventral rows of spinules (Fig. 3B). Anal segment 0.7 times as long as wide. Dimensions and armature of caudal rami as for female.

First antenna 5-segmented by fusion of the equivalent female segments 1 to 4, 5 and 6, 7 and 8, 9 and 10, 11 to 14; relative lengths 24: 9: 24: 19: 24; armature I–2; II–2; III–6; IV–ae; V–5 (Fig. 3C). Remaining limbs similar to those of female.

REMARKS. This species is unusual insofar as the maxilliped is not sexually dimorphic. It is assigned to the genus *Stenopontius* because of the lack of an exopodite to the second antenna, the five-segmented urosome, leaf-like fifth leg and the small exopodite of the first maxilla. It differs from both of the species hitherto described. The caudal rami are much longer than those of *S. parvus* Boxshall, 1990 and the first antenna has many more segments (8 in *S. parvus*), nor are the leg spines recessed (1990: figure 13D, E). This species shares the terminal armature of the first exopodite with *S. humesi* Murnane, 1967, II + 4, but differs again in the segmentation of the first antenna, the gross morphology of the siphon (more slender in *S. humesi*) and the armature of the fifth leg: 3 setae in *S. humesi*. The leg setae are not divided as they are in *S. humsei*.

Family ASTEROCHERIDAE Giesbrecht

Sinopontius punctatus *Boxshall, 1990*

Fig. 3D–F

Sinopontius punctatus Boxshall, 1990, pp. 529–533, figs 3D–F, 4, 5.

A male and a female were found in a purple-black sponge collected at a depth of 5–10m at Chek Kon Tau on 8 April 1986. They were recognised by body size (0.48 and 0.47m respectively), the rounded body shape (Fig. 3D), 19-segmented first antenna of the female, the unsegmented mandibular palp and the much reduced armature of the natatory legs. This species is distinguished from *S. aesthetascus* Boxshall, 1990, also described from Hong Kong specimens, by the armature of the second and third exopodites: the internal margins of the terminal segments are unarmed in *S. punctatus* and each has a single seta in *S. aesthetascus*. The specimens also exhibited the major details of the pore signature pattern drawn by Boxshall (Fig. 3E). The caudal rami are long, another useful diagnostic character. The exopodite of the second antenna has 2 terminal setae (Fig. 3F), but the third seta described by Boxshall may have been lost in dissection.

The BM(NH) registration numbers of these specimens are 1989.197 and 198.

ASTEROCHERES Boeck, 1859

The morphology of *Asterocheres* is well-defined and as Stock (1975) has noted, it is very coherent. The genus contains 48 species including those described below. They share a distal aesthetasc on the first antenna, although the exact position varies, a second antenna with a single-segmented exopodite and an endopodite tipped with a long curved hook and 2 setae. The mandibular palp is usually 1- sometimes 2-segmented; the stylet is long and pointed. The other mouthparts are more or less uniform throughout the genus with few exceptions and the armature of the natatory legs is constant:

	Coxa	Basis	Endopodite	Exopodite
Leg 1	0–1	1–1 or I	0–1; 0–2; 1,2,3	I–1; I–1; III, 2,2
Leg 2	0–1	1–0	0–1; 0–2; 1,2,3	I–1; I–1; III, I,4
Leg 3	0–1	1–0	0–1; 0–2; 1,1+I,3	I–1; I–1; III,I,4
Leg 4	0–1	1–0	0–1; 0–2; 1,1+I,2	I–1; I–1; III,I,4

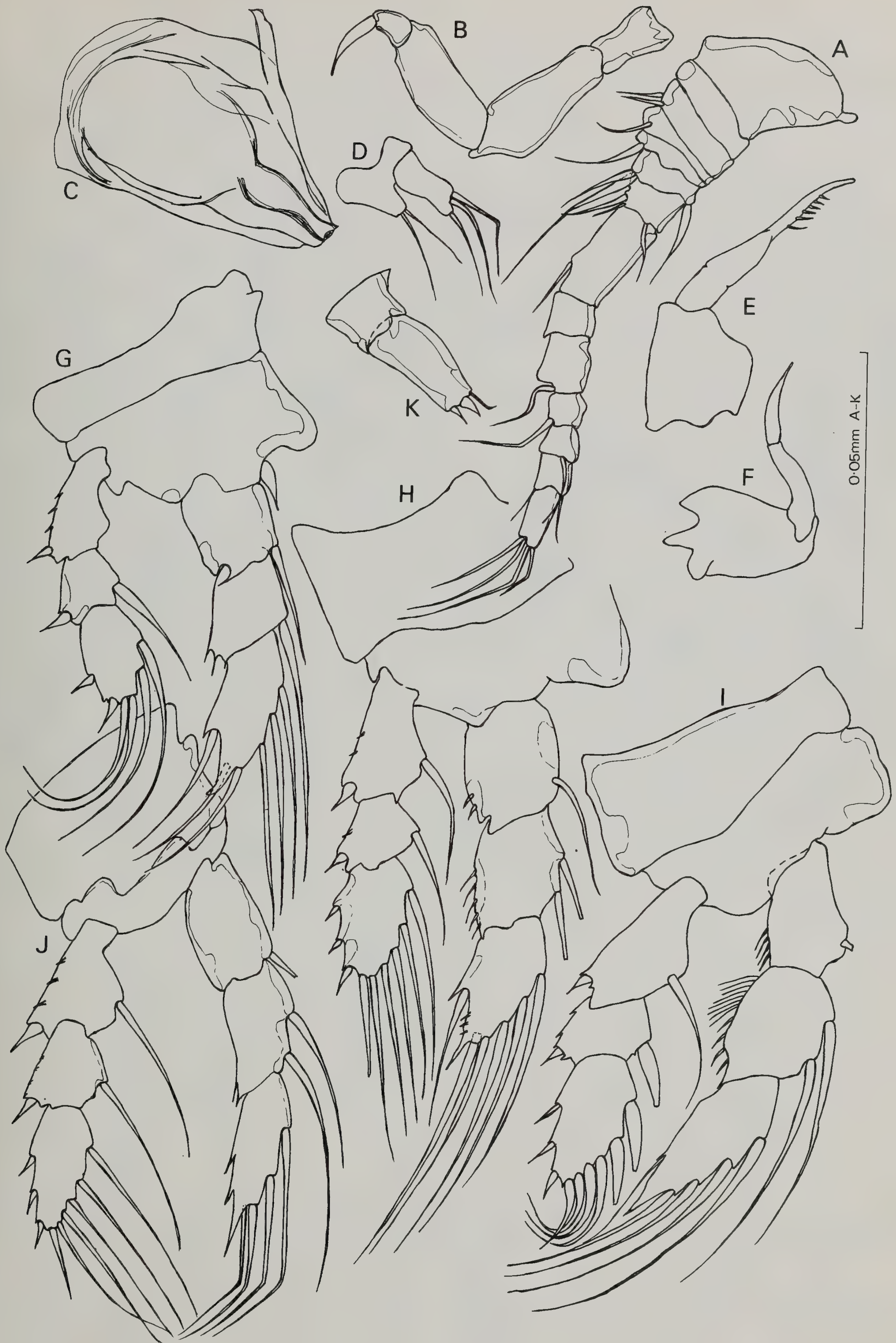


Fig. 2 *Stenopontius boxshalli* n. sp. ♀, holotype. A. First antenna; B. Second antenna; C. Siphon; D. First maxilla; E. Second maxilla; F. Maxilliped; G. First leg; H. Second leg; I. Third leg; J. Fourth leg; K. Fifth leg.

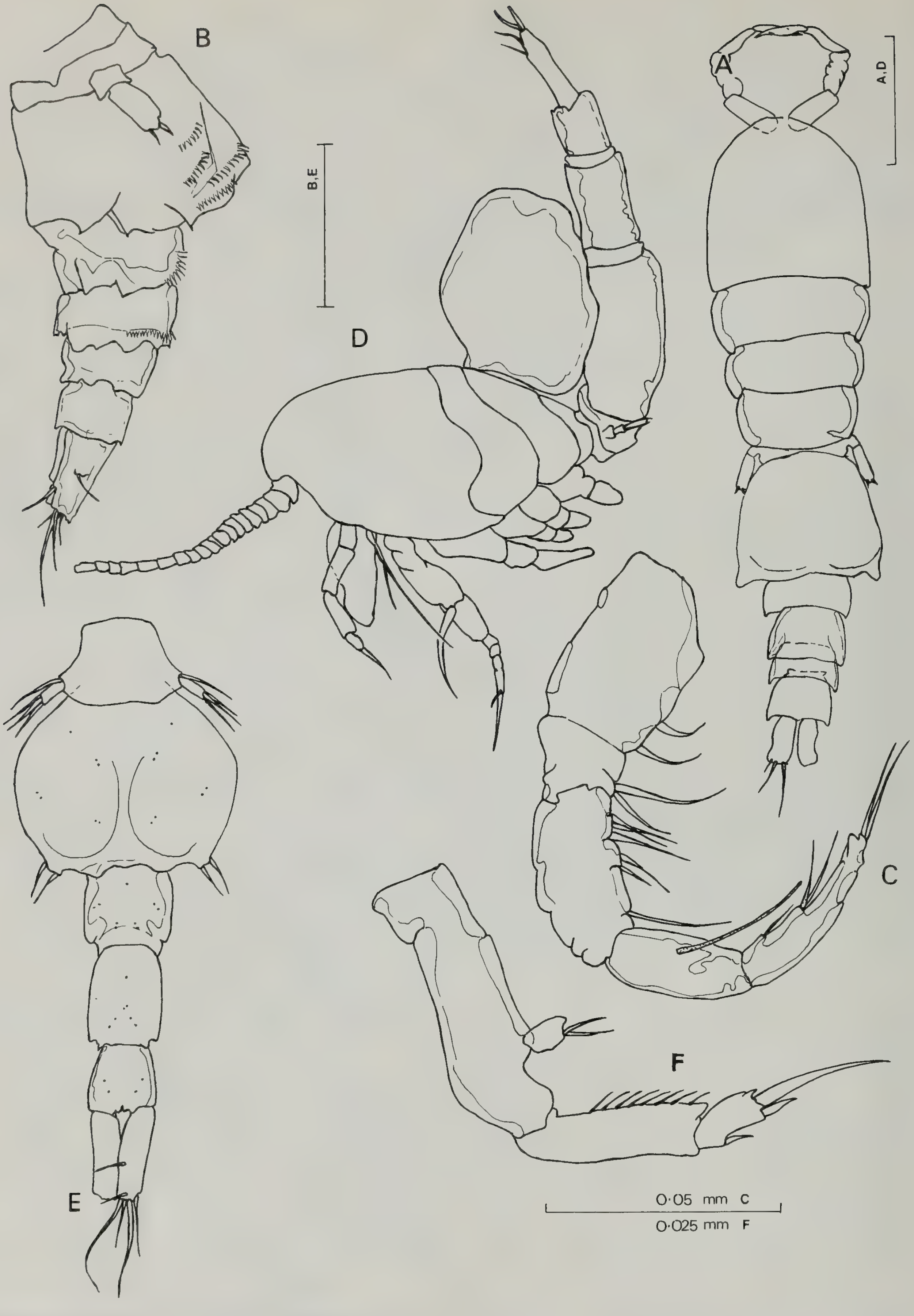


Fig. 3 *Stenopontius boxshalli* n. sp. ♂ A–C, paratype. A. Adult, dorsal view; B. Urosome, lateral view; C. First antenna; *Sinopontius punctatus* ♀. D. Adult, lateral view; ♂. E. Urosome, dorsal view; F. Second antenna. Scale bars = 0.1mm, except C, F.

There is a spine on the inner surface of the first basis, sometimes hard to pick out and not found for all species, but nevertheless it is probably universal in the genus. The fifth leg is single-segmented in both sexes and leaf-like, it has 1 subterminal and 2 terminal setae; there is also a seta nearby on the body segment. The prosome is 4-segmented, the first pedigerous segment is fused with the head. The rostrum is small. The female urosome is 4-segmented and the male urosome is 5-segmented, excluding the caudal rami. The caudal rami have 4 each terminal and 2 dorsal setae.

Individual species are separable on body shape, the number of segments in the female first antenna, the siphon

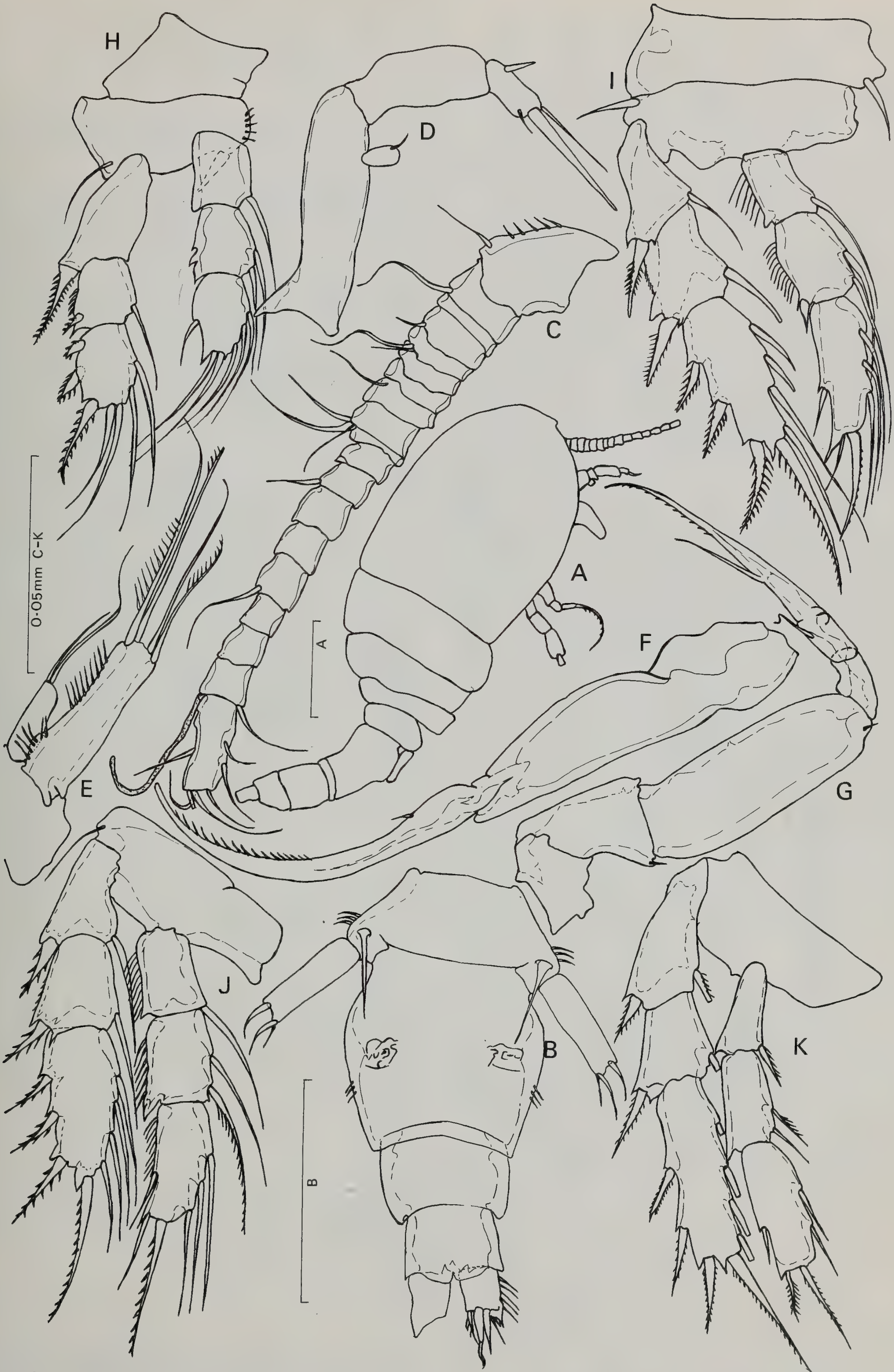


Fig. 4 *Asterocheres hongkongensis* n. sp. ♀, holotype. A. Adult, lateral view; B. Urosome, dorsal view; C. First antenna; D. Second antenna; E. Endopodite, first maxilla; F. Second maxilla; G. Maxilliped; H. First leg; I. Second leg; J. Third leg; K. Fourth leg. Scale bars = 0.1mm, except C-K.

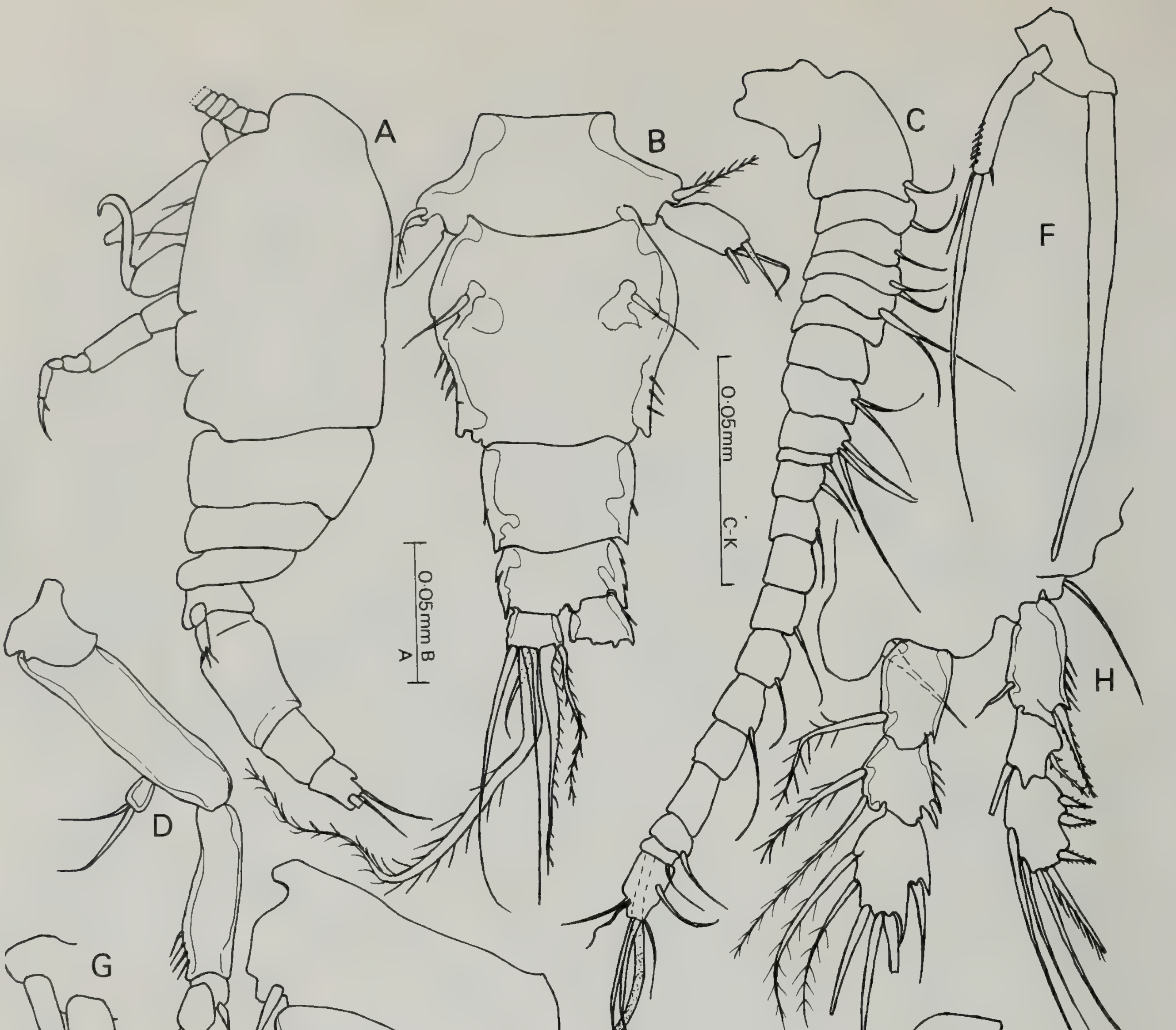

A
B
C
D
E
F
G
H
I
J
K
0·05mm B
A
0·05mm
C-K

Fig. 5 *Asterocheres bulbosus* n. sp. ♀, holotype. A. Adult, lateral view; B. Urosome, dorsal view; C. First antenna; D. Second antenna; E. Siphon; F. Mandible; G. First maxilla; H. First leg; I. Second leg; J. Third leg; K. Fourth leg. Scale bar A = 0.1mm.

length, length to width ratio of the fifth leg and caudal rami and the shape of the female genital segment. There is no comprehensive key to this genus, although one is badly needed.

Asterocheres hongkongensis *n. sp.*

Fig. 4A–K

Material examined. Holotype ♀ from orange sponge collected at a depth of 8m at Chek Chau on 10 April 1986 BM(NH) registration number 1989.199.

Etymology. The specific name refers to the type locality.

Female. Characteristic asterocherid shape, dorso-ventrally flattened, rounded cyclopoid, 0.50mm long (Fig. 4A). Prosome 1.8 times as long as urosome, relative lengths of prosome segments 64: 17: 12: 7; relative lengths of urosome segments 17: 40: 19: 15: 9 (Fig. 4B). Genital segment tapering only slightly towards posterior margin; widest point at level of genital apertures, genital apertures dorso-laterally placed; genital segment equal in length and width measured at widest point; lateral tuft of setules posterior to each aperture. Anal segment 0.8 times as long as wide. Caudal rami 1.1 times as long as wide, trapezoid in dorsal view with postero–lateral spinose projection.

First antenna 19-segmented (Fig. 4C); relative lengths 10: 5: 3: 3: 3: 3: 3: 4: 5: 1: 3: 6: 6: 6: 6: 7: 6: 7: 13; armature apparently I–1+setules; II–1; III–0; IV–1; V–2; VI–0; VII–0; VIII–1; IX–3; X–0; XI–0; XII–1; XIII–0; XIV–0; XV–1; XVI–0; XVII–0; XVIII–1+ae; XIX–7 (some elements may be missing). 3 terminal elements of second antennal endopodite accompanied by external spine (Fig. 4D). Siphon short, not reaching maxilliped base, pyriform. Armature of first and second maxillae, maxilliped and natatory legs illustrated (Fig. 4E–K), typical of genus. Spines on external margin of second segment of first endopodite with row of accompanying setules. Fifth leg extending beyond level of genital apertures, about 3 times as long as wide.

Remarks. *Asterocheres hongkongensis* resembles *A. indicus* Sewell, 1949, and *A. alter* Eiselt, 1965. It differs from the former in body size, the relative lengths of the segments of the first antenna and according to Sewell's figure, the length of the fifth leg (1949: figure 10B). The female of *A. alter* is not known, however disregarding the dimorphic characters of this genus, the species differ in the robustness of the fourth endopodite; Eiselt (1965) noted that this limb is reduced in *A. alter*. *Asterocheres alter* also lacks the postero–lateral projection of the caudal rami (1965: figure 2m).

Asterocheres bulbosus *n. sp.*

Figs 5A–6D

Material examined. Holotype ♀, allotype, 9 ♀♀ and 8 ♂♂ paratypes from purplish sponge collected at a depth of 10m at Gau Tau on 18 April 1986. BM(NH) registration numbers 1989.200 (holotype), 1989.201 (allotype), 1989.202–218.

Etymology. This species is so named because of the distinctively bulbous caudal setae.

Female. Cyclopoid shape, dorso-ventrally flattened, 0.47mm long, range 0.42 to 0.50mm (Fig. 5A). Prosome 1.9 times as long as urosome, relative lengths of prosome segments 66: 18: 9: 7; relative lengths of urosome segments 22: 39: 21: 11: 7 (along mid-line of caudal rami) (Fig. 5B). Genital segment tapering posteriorly; widest point anterior to genital apertures, genital apertures dorso-laterally placed; genital segment 0.8 times as long as wide. Caudal rami 0.6 times as long as wide, expanding to greater width posteriorly; caudal setae bulbous.

First antenna 21-segmented (Fig. 5C); relative lengths of segments 16: 4: 4: 4: 3: 3: 5: 5: 4: 1: 4: 5: 6: 5: 6: 6: 6: 7: 3: 2: 1; armature apparently I–1; II–1; III–1; IV–2; V–2; VI–0; VII–0; VIII–2; IX–3; X–1; XI–1; XII–1; XIII–0; XIV–1; XV–1; XVI–1; XVII–0; XVIII–0; XIX–1; XX–1+ae; XXI–6. Distal external surface of third segment of second antenna with row of setules (Fig. 5D). Siphon short, not reaching maxilliped base, pyriform (Fig. 5E). Mandibular palp 1-segmented with 2 terminal setae, 1 long and robust, 1 short and weak; stylet long, curved and unarmed (Fig. 5F). Inner lobe of first maxilla comparatively long and slender (Fig. 5G). Second maxilla and maxilliped typical of genus. Natatory legs also typical of genus (Fig. 5H–K). Fifth leg about twice as long as wide (Fig. 5B).

Male. Cyclopoid body shape, dorso-ventrally flattened, 0.37mm long, range 0.32 to 0.40mm (Fig. 6A). Prosome 1.7 times as long as urosome, relative lengths of prosome segments 66: 13: 13: 8; relative lengths of urosome segments 14: 38: 14: 12: 12: 10 (along mid-line of caudal rami) (Fig. 6B). Genital segment rotund, widest at mid-point, 0.6 times as long as wide, genital lappets represented by postero-lateral seta on each side. Anal segment half as long as wide. Caudal rami equal in length and width, expanding to greater width posteriorly; caudal setae bulbous at bases.

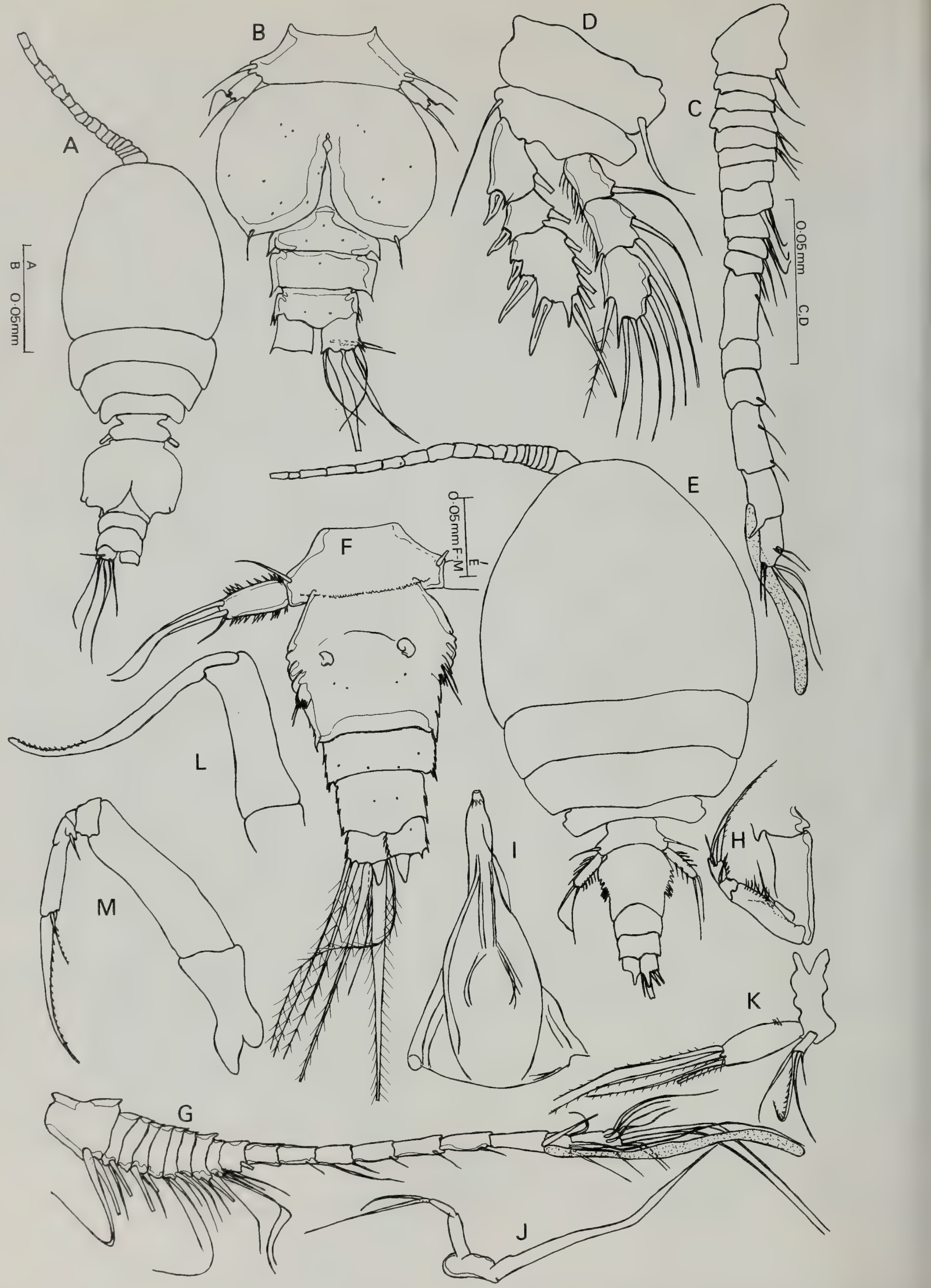
First antenna 17-segmented by fusion of female segments 12 and 13, 16 and 17, 18 to 20 (Fig. 6C); penultimate segment with distal hook; relative lengths of segments 15: 3: 3: 4: 3: 3: 4: 5: 4: 1: 4: 12: 5: 6: 10: 10: 8; armature indistinct, apparently I–1; II–1; III–0; IV–2; V–2; VI–0; VII–0; VIII–2; IX–2; X–1; XI–2; XII–1; XIII–0; XIV–1; XV–2; XVI–ae; XVII–6. Remainder of mouthparts and natatory legs similar to female, except exopodite of second leg where external spines of male are bluntly spatulate (compare Figs 5I and 6D). Fifth leg reduced to short segment delimited from body segment, with 2 terminal setae.

Remarks. *Asterocheres bulbosus* resembles *A. aesthetes* Ho, 1984 and *A. hongkongensis*. However the females of these each have a 19-segmented first antenna and *A. aesthetes* has a highly characteristic aesthetasc on the second maxilla. The male of *A. alter* is similar to that of *A. bulbosus* but has longer caudal rami and a 2-segmented mandibular palp. The proportional lengths of the segments of the first antenna also differ. Females of this species differ from *A. hongkongensis* in several ways, notably in the slenderness of the endopodite of the first maxilla, the short fifth leg, and the bulbous caudal setae.

Asterocheres rotundus *n. sp.*

Figs 6E–7H

Material examined. Holotype ♀ from purplish sponge collected at a depth of 5–10m at Gau Tau on 18 April 1986. 2 ♀♀ and 2 ♂♂ paratypes from reddish-purple sponge collected at a depth of 2m at Peng Chau on 15 April 1986; 1 ♀


A
B
C
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0·05mm C,D
0·05mm F–M
E

Fig. 6 *Asterocheres bulbosus* n. sp. ♂. A–D, paratype. A. Adult, dorsal view; B. Urosome, ventral view; C. First antenna; D. Second leg; *A. rotundus* n. sp. ♀. E–M, holotype. E. Adult, dorsal view; F. Urosome, dorsal view; G. First antenna; H. Second antenna; I. Siphon; J. Mandible; K. First maxilla; L. Second maxilla; M. Maxilliped. Scale bars A, E = 0.1mm.

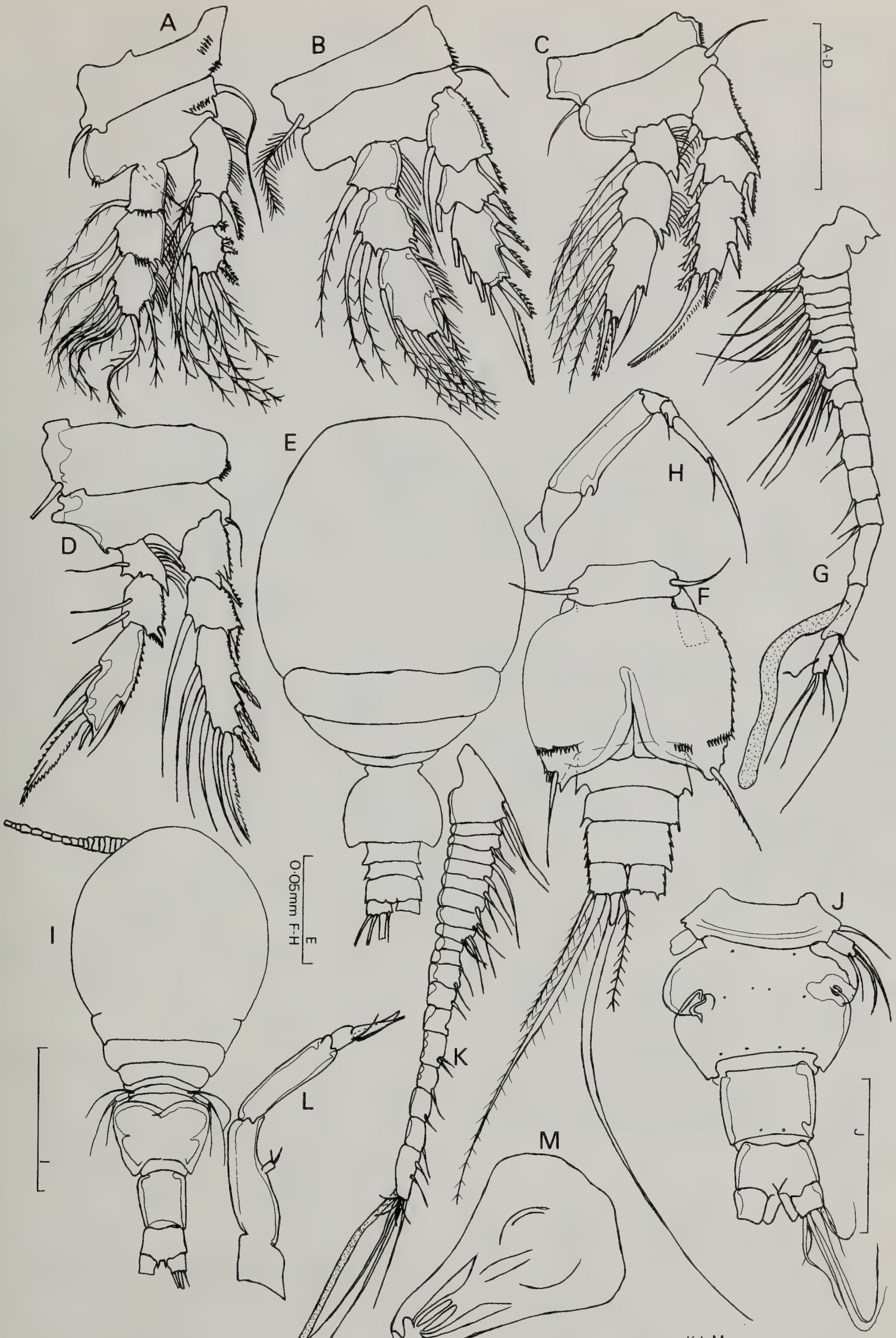

Fig. 7 *Asterocheres rotundus* n. sp. ♀. A–D, holotype. A. First leg; B. Second leg; C. Third leg; D. Fourth leg; ♂. E–H, paratype. E. Adult, dorsal view; F. Urosome, ventral view; G. First antenna; H. Maxilliped; *Asterocheroides sinensis* n. gen. n. sp. ♀. I–M, holotype. I. Adult, dorsal view; J. Urosome, dorsal view; K. First antenna; L. Second antenna; M. Siphon. Scale bars = 0.1mm, except F–H.

and 1 ♂ paratypes from the sponge *Ricinia* sp. collected at a depth of 15m at Chik Chau on 6 April 1986. BM(NH) registration numbers 1989.219 (holotype), 1989.220–225.

ETYMOLOGY. This species is named according to the rounded body shape.

FEMALE. Laterally expanded cyclopoid shape, head angular, dorso-ventrally flattened, 0.62mm long, range 0.59 to 0.66mm (Fig. 6E). Prosome 2.2 times as long as urosome, relative lengths of segments 67: 14: 15: 4; relative lengths of urosome segments 16: 43: 12: 19: 10 (along mid-line of caudal rami), posterior and lateral margins setulose. Genital segment robust and flask-shaped (Fig. 6F); widest point anterior to genital apertures, genital apertures dorso-laterally placed; genital segment 0.7 times as long as wide, segment laterally infolded and with tuft of spinules and setules posterior to infolds; anal segment 0.7 times as long as wide. Caudal rami equal in length and width, with spinules on both lateral margins.

First antenna 19-segmented (Fig. 6G); relative lengths 4: 3: 3: 2: 2: 2: 2: 4: 2: 6: 7: 8: 8: 8: 9: 10: 10: 3: 7; armature I–2; II–2; III–1; IV–2; V–2; VI–2; VII–1; VIII–2; IX–5; X–1; XI–0; XII–2; XIII–1; XIV–1; XV–1; XVI–1; XVII–1+ae; XVIII–3; XIX–8. Third and terminal segments of second antenna setulose, terminal seta also setulose (Fig. 6H). Siphon reaching beyond maxilliped basis, but not to basis of first leg, tubiform (Fig. 6I). Other mouthparts typical of genus (Fig. 6J–M).

External spine on first segment of first leg enlarged and robust; internal exopodite margins fringed with long setules (Fig. 7A–D). Fifth leg about twice as long as wide (Fig. 6F).

MALE. Laterally expanded cyclopoid shape, head angular, dorso-ventrally flattened, 0.49mm long, range 0.48 to 0.50mm (Fig. 7E). Prosome 1.9 times as long as urosome (figured specimen slightly telescoped), relative lengths of prosome segments 59: 23: 11: 7; relative lengths of urosome segments 16: 41: 12: 9: 14: 8 (along mid-line of caudal rami). Genital segment with relatively large genital lappets, bearing long robust spine and row of marginal spinules, segment with pronounced anterior shoulders, 0.8 times as long as wide (Fig. 7F). Anal segment and caudal rami 0.7 times as long as wide.

First antenna 17-segmented, by fusion of female segments 16 and 17, 18 and 19 (Fig. 7G); penultimate segment with distal hook; antenna geniculate, articulated between segments 15 and 16; relative lengths of segments 5: 3: 2: 2: 2: 2: 2: 4: 2: 7: 8: 7: 9: 6: 15: 13: 11, armature similar to that of female but with aesthetasc on penultimate segment. Mandible, first and second maxilla similar to those of female. Second segment of maxilliped with proximal hooked process (Fig. 7H). Natatory legs similar to those of female. Fifth leg typical of genus.

REMARKS. This species is easily distinguished from the previous two by the angular head, and the longer, thinner siphon. In most species of *Asterocheres* the siphon is pyriform, in some species it is tubiform and in a few species the tube reaches beyond the level of the basis of leg 2. *Asterocheres rotundus* is one of the intermediate group in which the tubiform siphon is shorter than this. This species is similar to the following on the base of the siphon, the 19-segmented female first antenna and body size (*A. ovalis* Sewell, 1949 is included although the siphon length is not known): *Asterocheres aesthetes* is distinguished by the aesthetasc on the basis of the second maxilla; *A. canui* Giesbrecht, 1897 is not well-known and the type description is poor, it is known only from the male which has a distinctive swollen seta on the outer ramus of the first maxilla, not found on *A. rotundus*; *A. halichondriae* Stock, 1966 has external spines on the fourth exopodite which are reduced in size and are smaller than those found here; *A. indicus* differs in having caudal rami which are longer than they are broad; *A. mucronipes* Stock, 1960 and *A. scutatus* Stock, 1966 are both more bulky-looking species, *A. mucronipes* has a longer exopodite on the second antenna; finally *A. ovalis,* known only from the male, has a genital segment which is about twice as wide as it is long, also the anal segment is longer in proportion to the preceding segment than in *A. robustus.* Of all the foregoing, *A. halichondriae* is the most similar in general appearance to *A. robustus.*

ASTEROCHEROIDES n. gen

DIAGNOSIS. Asterocheridae; body cyclopoid, prosome 4-segmented, urosome 4-segmented in female, excluding caudal rami, 5-segmented in male. First antenna 19-segmented in female with aesthetasc on distal segment; 17-segmented in male, aesthetascs on segments 16 and 17. Second antenna with single-segmented exopodite, bearing 2 setae; endopodite with seta and robust claw. Siphon short and conical. Mandibular palp single-segmented with 2 terminal setae. Second maxilla 3-segmented with thick terminal hook. Maxilliped 5-segmented with terminal claw. Natatory legs all biramous and 3-segmented, each exopodite bearing 3 external spines on terminal segment; internal spine on first basis; terminal segment on fourth endopodite with setal formula 0, 1, 2.

ETYMOLOGY. Superficially at least, this genus resembles *Asterocheres* and the root of the name is used accordingly.

Asterocheroides sinensis *n. gen. n. sp.*

Figs 7I–8J

MATERIAL EXAMINED. Holotype ♀, allotype, 6 ♀♀ and 5 ♂♂ paratypes from the sponge *Ricinia* sp. collected at a depth of 15m at Chik Chau on 6 April 1986. BM(NH) registration numbers 1989.226 (holotype), 1989.227 (allotype), 1989.228–238.

ETYMOLOGY. The specific name comes from the type locality.

FEMALE. Characteristic asterocherid, rounded cyclopoid shape; burgundy red in colour; 0.32mm long, range 0.27 to 0.34mm (Fig. 7I). Prosome 1.4 times as long as urosome; head laterally expanded with point of maximum width half way between rostrum and posterior margin; head incompletely fused to following segment; rostrum inconspicuous; relative lengths of prosome segments 79: 8: 8: 5; relative lengths of urosome segments 13: 38: 24: 16: 9 (along mid-line of caudal rami). Genital segment very broad with distinct antero-lateral shoulders, 0.6 times as long as wide; genital apertures in lateral infoldings of segment well just anterior to mid-point, paired cuticular pores clearly visible (Fig. 7J). Anal segment 0.6 times as long as wide, excluding ventral flap. Caudal rami about equal in length and width measured along outer edge, shorter along inner edge; 6 terminal and sub-terminal setae; 2 shield-like process posteriorly projecting between rami.

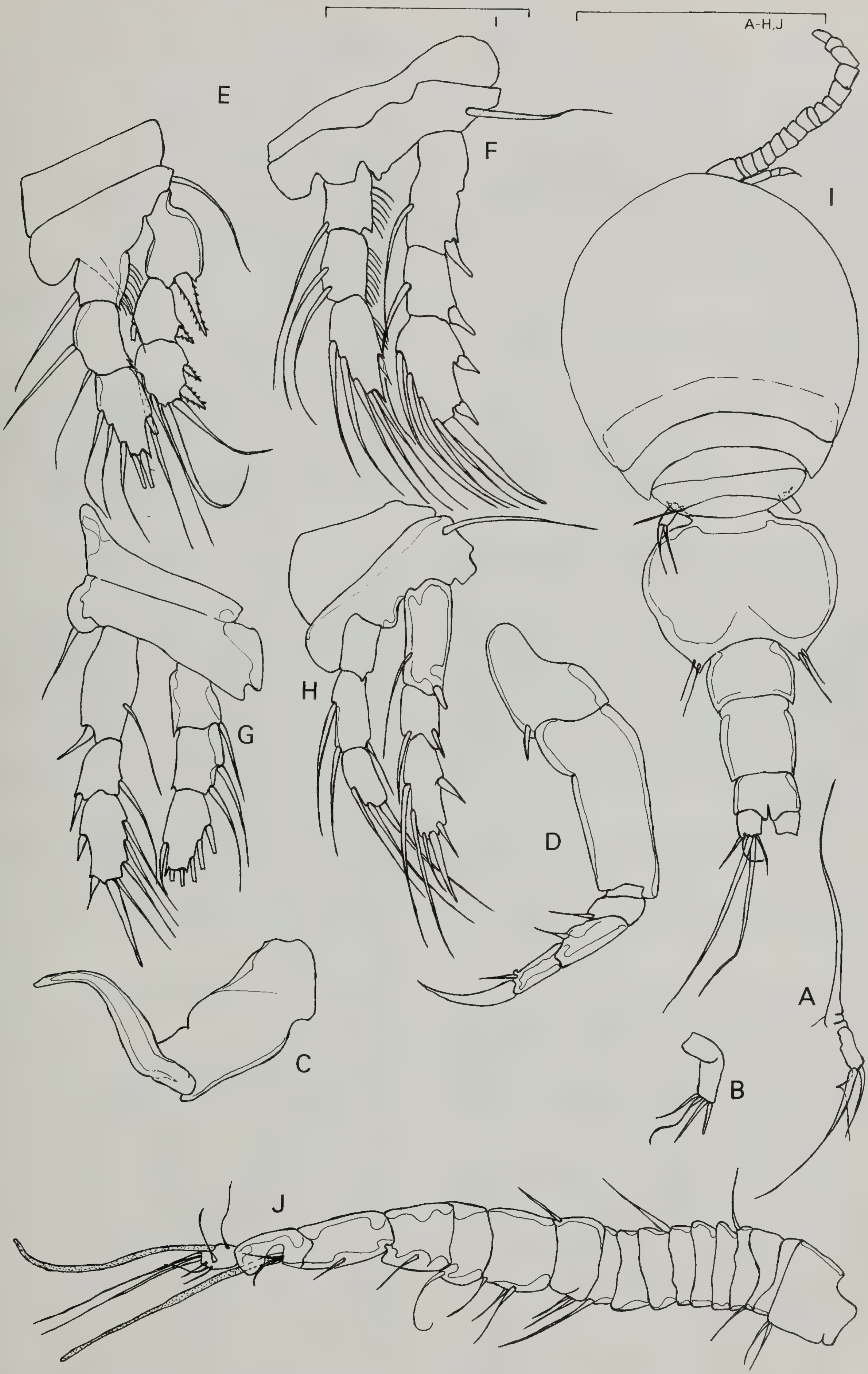

Fig. 8 *Asterocheres sinensis* n. gen. n. sp. ♀. A–H, holotype. A. Mandible; B. Outer lobe, first maxilla; C. Second maxilla; D. Maxilliped; E. First leg; F. Second leg; G. Third leg; H. Fourth leg; ♂. I, J, paratype. I. Adult, dorsal view; J. First antenna. Scale bars = 0.1mm.

First antenna 19-segmented (Fig. 7K); relative lengths 7: 2: 2: 3: 4: 4: 5: 4: 3: 4: 3: 5: 6: 7: 7: 7: 7: 7: 13; armature I–3; II–0; III–2; IV–1; V–1; VI–2; VII–1; VIII–2; IX–3; X–0; XI–1; XII–1; XIII–1; XIV–0; XV–2; XVI–1; XVII–1; XVIII–1; XIX–7+ae. Endopodite of second antenna with short robust spine, thinner spine and seta distally; short, single-segmented exopodite with 2 terminal setae (Fig. 7L). Siphon conical (Fig. 7M). Mandibular palp short, single-segmented with 1 long and 1 short terminal seta; stylet pointed, jointed at base (Fig. 8A). First maxilla damaged in dissection, outer lobe with 4 terminal setae (Fig. 8B). Second maxilla robust with short thick terminal claw (Fig. 8C). Maxilliped 5-segmented with terminal heavy claw (Fig. 8D).

Armature of natatory legs (Fig. 8E–H):

	Coxa	Basis	Endopodite	Exopodite
Leg 1	0–0	1–I internal	0–1; 0–2; 1,1,4	I–0; I–1; II,2,2
Leg 2	0–0	1–0	0–1; 0–2; 1,1,4	I–1; I–1; II,I,4
Leg 3	0–0	1–0	0–1; 0–2; 1,1,4	I–1; I–1; II,1,4
Leg 4	0–0	1–0	0–0; 0–2; 0,1,2	I–1; I–1; II,I,4

Fifth leg single, cylindrical segment with 3 long terminal and sub-terminal setae reaching beyond level of genital apertures; seta on body nearby.

MALE. Similar in body shape to female, 0.33mm long, range 0.30 to 0.35mm (Fig. 8I). Prosome 1.1 times as long as urosome (figured specimen telescoped); relative lengths of prosome segments 67: 20: 8: 5; relative lengths of urosome segments 13: 34: 16: 20: 10: 7 (along mid-line of caudal rami). Genital segment rotund, 0.6 times as long as wide, cuticular pores as for female; genital lappets small and rounded, 2 spines on each. Anal segment 0.7 times as long as wide. Caudal rami as for female.

First antenna 17-segmented (Fig. 8J), by fusion of female segments 15 and 16, and 17 with 18; relative lengths of segments 9: 2: 4: 3: 3: 4: 3: 4: 4: 3: 7: 10: 6: 9: 12: 10: 7; armature similar to that of female except segment 16 with invagination bearing aesthetasc. Remainder of limbs similar to those of female.

REMARKS. This species is typically asterocheroid in possessing the single-segmented exopodite of the second antenna, together with the terminal claw and accompanying single seta of the endopodite. This species also has the characteristic mandibular palp, 3-segmented biramous natatory legs (not universal in the family) and 4-segmented female urosome. The Asterocheridae share a many-segmented first antenna, here there are 19 segments in the female.

In Table 1 *Asterocheroides* is compared to some morphologically similar genera. Like *Asteropontopsis* Stock, 1987 it lacks an inner seta on the first segment of the first exopodite, the endopodite of the second antenna resembles *Asteropontius* Thompson & Scott, 1903 and *Asteropontopsis* but the reduced armature distinguishes *Asterocheroides*. It is most morphologically akin to *Asteropontopsis* but the latter has a distinctive pair of hyaline lobes on the distal part of the siphon, and also the first antenna has a sub-terminal aesthetasc (terminal in *Asterocheroides*). Stock (1987) states that the differences between *Asteropontius* and *Asteropontopsis* are slight but sufficient to warrant separation of their respective species into separate genera. *Asterocheroides* is erected on a similar basis.

Table 1 A comparison of some morphologically similar genera of asterocherids.

	A1	A2	Man	ex 1	ex 2	ex 4	en 4	P5
Asterocheres Boech, 1859	19–20	2+I	1/2(2)	I–1	t	III, I, 4	1+I,2	v
Asterocheroides n. gen.	19	1+c	1 (?)	I–0	t	II,I,4	2,1	s
Asteropontius Thompson and Scott, 1903	19–20	1+c	1 (1)	I–1	t	III,I,4	1+I,2	s
Asteropontoides Stock, 1975	18	2+I	? (?)	I–1	L	III,I,3	I,2	e
Asteropontopsis Stock, 1987	19	1+c	1 (1)	I–0	t	II,I,4	1+I,2	l

A1, number of segments female first antenna. A2, armature endopodite second antenna: c = claw. Man, segmentation mandibular palp (armature). ex 1, armature first segment first exopodite. ex 2, shape second segment first exopodite: t = trapezoid, L = l-shaped. ex 3, armature third segment fourth exopodite. en 4, armature third segment fourth endopodite. P5, size basal segment fifth leg: v = variable, s = small, e = elongate, l = large and robust.

SIPHONOPONTIUS n. gen.

DIAGNOSIS. Asterocheridae; body cyclopoid, prosome 5-segmented, urosome 4-segmented in female, excluding caudal rami. First antenna 20-segmented with terminal aesthetasc. Second antenna with single-segmented exopodite, bearing 2 setae; endopodite with robust terminal spine and thick claw. Siphon pyriform with bulbous tip. Mandibular palp single-segmented with terminal seta. First maxilla: outer lobe with 4 terminal elements, inner lobe with 2. Second maxilla tipped with robust, recurved claw. Maxilliped 5-segmented with terminal claw. Natatory legs biramous, each 3-segmented except fourth endopodite 2-segmented; terminal armature fourth endopodite 2+I. Male not known.

ETYMOLOGY. This genus is so named because of the distinctive shape of the siphon of the type-species.

Siphonopontius robustus *n. gen. n. sp.*

Fig. 9A–L

MATERIAL EXAMINED. Holotype ♀, 2 ♀♀ paratypes from an orange sponge collected at a depth of 8m at Chek Chau on 10 April 1986. BM(NH) registration numbers 1989.239 (holotype), 1989.240–241. 8 ♀♀ from reddish-purple sponge collected at a depth of 2m at Peng Chau on 15 April 1986. BM(NH) registration numbers 1989.242–249.

FEMALE. Cyclopoid shape, 0.36 mm long, range 0.33 to 0.42mm (Fig. 9A). Prosome twice as long as urosome; head 1.2 times as long as wide; head not fused to following segment, therefore prosome 5-segmented, but segmentation indistinct, relative lengths 52: 16: 19: 9: 4; rostrum small and rounded; relative lengths of urosome segments 19: 47: 12: 17: 5 (along mid-line of caudal rami). Genital segment short and robust, not greatly expanded, 0.7 times as long as wide, genital apertures dorso-laterally placed at position of maximum width (Fig. 9B); paired egg sacs with single eggs.

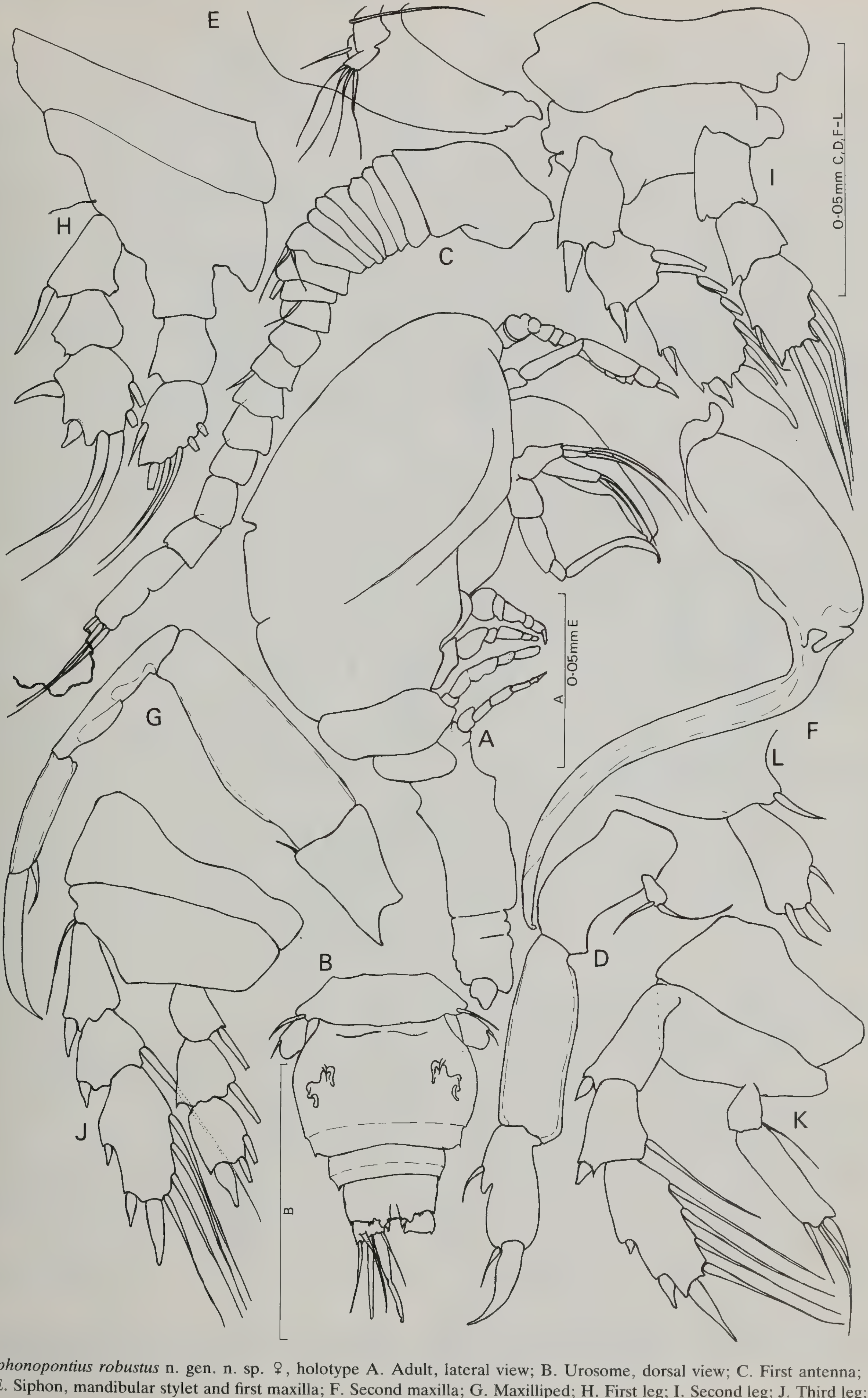

Fig. 9 *Siphonopontius robustus* n. gen. n. sp. ♀, holotype A. Adult, lateral view; B. Urosome, dorsal view; C. First antenna; D. Second antenna; E. Siphon, mandibular stylet and first maxilla; F. Second maxilla; G. Maxilliped; H. First leg; I. Second leg; J. Third leg; K. Fourth leg; L. Fifth leg. Scale bars A, B = 0.1mm.

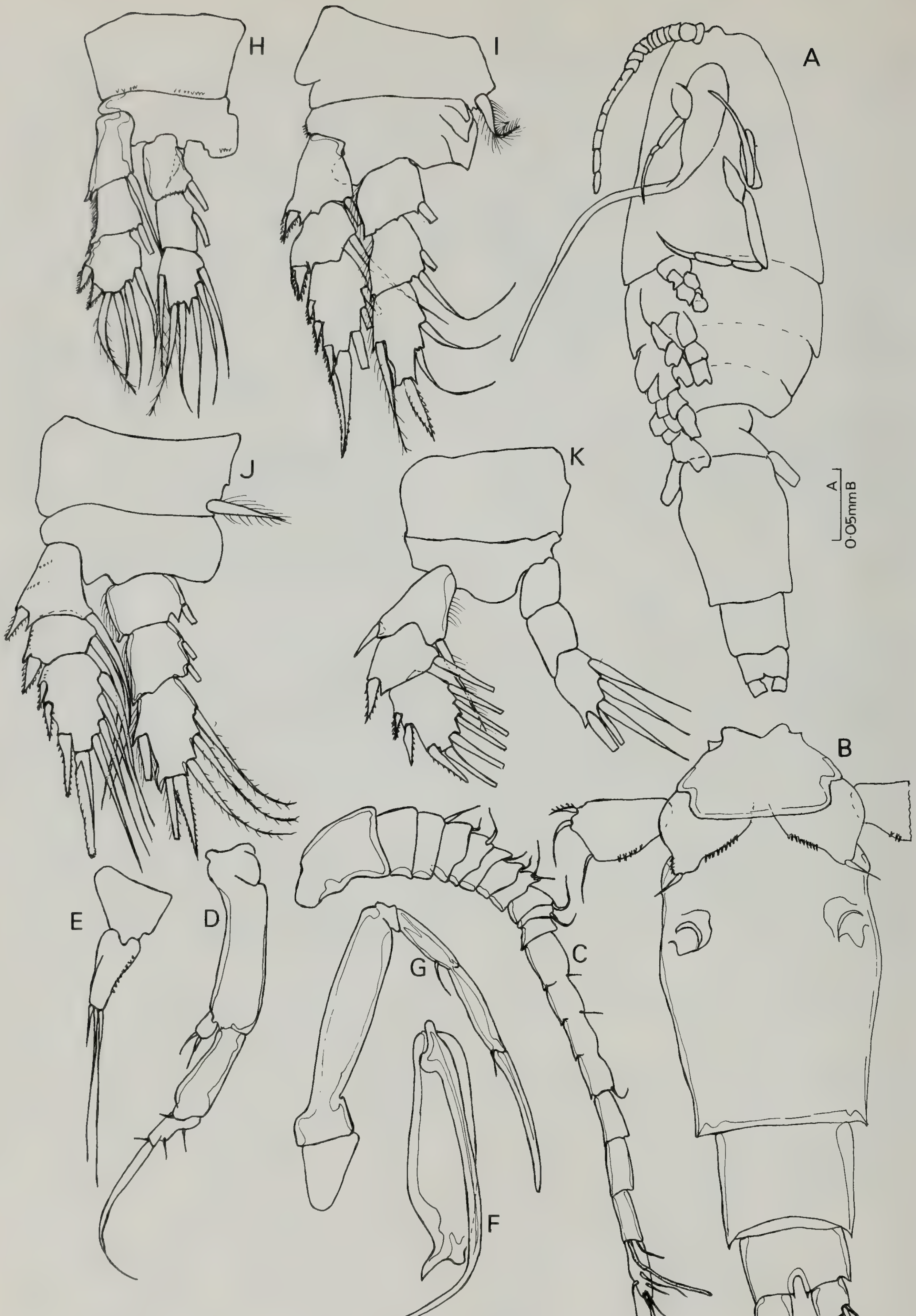

Fig. 10 *Scottocheres stocki* n. sp. ♀, holotype. A. Adult, ventral view; B. Urosome, dorsal view; C. First antenna; D. Second antenna; E. Inner lobe, first maxilla; F. Second maxilla; G. Maxilliped; H. First leg; I. Second leg; J. Third leg; K. Fourth leg. Scale bars = 0.1mm, except B.

Anal segment half as long as wide measured along mid-line, 0.4 times as long as wide measured along lateral margin, medial posterior processes accounting for difference. Caudal rami also irregular in shape. 0.3 times as long as wide along inner margin and 0.7 times along outer margin; armature 4 terminal setae of varying lengths, largest seta jointed, and 1 dorsal seta.

First antenna 20-segmented, segmentation indistinct (Fig. 9C); relative lengths 15: 3: 2: 2: 2: 3: 2: 4: 5: 3: 3: 4: 5: 6: 6: 6: 6: 7: 6: 10; armature uncertain, indistinct but bearing terminal aesthetasc. Exopodite of second antenna single-segmented with 2 terminal setae; endopodite with short thick terminal spine and thick claw, external margin of third segment dentate (Fig. 9D). Siphon short, pyriform with bulbous tip. Mandible with single-segmented palp bearing 1 terminal seta; stylet unarmed and pointed (Fig. 9E). Outer lobe of first maxilla with 4 terminal setae (Fig. 9E); inner lobe with 2 terminal setae. Second maxilla with long recurved claw (Fig. 9F). Maxilliped indistinctly 5-segmented with short terminal claw and seta (Fig. 9G).

Armature of natatory legs (Fig. 9H–K):

	Coxa	Basis	Endopodite	Exopodite
Leg 1	0–0	1–0	0–0; 0–0; 1,1,4	I–0; I*–0; II,2,2
Leg 2	0–0	1–0	0–1; 0–1; 1,2,2	I–0, I–1; II,I,4
Leg 3	0–0	1–0	0–1; 0–1; 0,I,2	I–0; I–1; II,I,4
Leg 4	0–0	0–0	0–1; 2+I	I–0; I–1; II,I,4

* missing from figured specimen

Spines on exopodites indistinctly flanged, those of first exopodite rounded. Fifth leg single-segmented, leaf-like; armature comprising 2 terminal and 1 sub-terminal setae (Fig. 9L).

Remarks. This genus can be grouped with *Discopontius* Nicholls, 1944 and *Peltomyzon* Stock, 1975 as they share many similarities in morphology. *Siphonopontius* can be assigned to the Asterocheridae on the same bases as *Asterocheroides* (cf), namely the many-segmented first antenna and the second antennal claw, the presence of the mandibular palp and the 4-segmented female urosome. However *Siphonopontius* shares a 2-segmented fourth endopodite with *Discopontius* and *Peltomyzon,* in *Asterocheroides* this limb is 3-segmented. In common with *Asterocheroides, Siphonopontius* has a terminal aesthetasc on the first antenna. This new genus differs from *Peltomyzon* in possessing a 3-segmented third endopodite, in Peltomyzon it is 2-segmented. It differs from *Discopontius* in having a single medial seta on the second segment of the second endopodite and no seta at all at the corresponding position on the first leg. *Discopontius* has 2 setae at each position. *Discopontius* is known only from the type species, *D. discoides*; in many ways it is very similar to *S. robustus,* but besides the above, it may be distinguished by the lateral expansions of the genital segment.

Scottocheres stocki n. sp.

Fig. 10 A–K

Material examined. Holotype ♀ from the sponge *Ricinia* sp. collected at a depth of 15m at Chik Chau on 6 April 1986. BM(NH) registration number 1989.250.

Etymology. This species is named after Professor Jan Stock in recognition of his extensive work on the Asterocheridae.

Female. Elongated and slender cyclopoid shape, 0.92mm long (Fig. 10A). Prosome 1.3 times as long as urosome; head equal in length and width, maximum width at posterior margin; rostrum small; relative lengths of prosome segments 58: 19: 12: 11; relative lengths of urosome segments 12: 54: 17: 11: 6. Genital segment almost uniform in width, tapering only slightly posteriorly, widest at position of dorso-laterally placed genital apertures; 1.8 times as long as wide (Fig. 10B). Anal segment 0.6 times as long as wide. Caudal rami equal in length and width, with 5 terminal and sub-terminal setae of varying lengths.

First antenna 19-segmented, segments 12 to 15 partially fused; relative lengths 6: 4: 5: 3: 2: 2: 3: 2: 2: 1: 5: 8: 6: 6: 8: 8: 8: 9: 12; armature I–0; II–0; III–1; IV–1; V–1; VI–1; VII–1; VIII–2; IX–1; X–1; XI–0; XII–1; XIII–1; XIV–0; XV–1; XVI–0; XVII–0; XVIII–1+ae; XIX–6 (Fig. 10C). Second antenna typically asterocherid: terminal endopodite segment with long hooked claw and 2 terminal spinules; exopodite single-segmented with 2 terminal setae (Fig. 10D). Siphon elongate, distally slim and tubiform, reaching genital segment (Fig. 10A). Mandibular stylet smooth, thin and equal in length to siphon. Inner lobe of first maxilla single-segmented with 3 terminal setae, row of denticles on outer margin (Fig. 10E). Second maxilla 2-segmented, unarmed (Fig. 10F). Maxilliped 5-segmented, third and fourth segments with distal spinules on inner angles, fifth segment produced as unarmed claw (Fig. 10G).

Armature of natatory legs (Fig. 10 H–K):

	Coxa	Basis	Endopodite	Exopodite
Leg 1	0–0	I internal–0	0–1; 0–1; 1,2,3	0–1; 0–1; II,2,2
Leg 2	0–I	0–0	0–1; 0–2; 1,I,2	I–1; I–1; III,I,3
Leg 3	0–I	0–0	0–1; 0–2; 1,1+I,3	I–1; I–1; III,I,4
Leg 4	0–0	0–0	0–0; 0–0; 0,2,3	I–1; I–1; III,1,4

Expodite spines flanged except for spatulate terminal spine of third leg. Fifth leg single-segmented and leaf-like; 3 distal spinules (Fig. 10B). Body segment bearing fifth leg also bearing posteriorly pointing ventral flanges, each with terminal spine flanked by rows of denticles.

Remarks. Stock produced a comprehensive key to the genera of the Asterocheridae (1987). This species is readily assigned to *Scottocheres* Giesbrecht, 1892. It is superficially similar to *S. elongatus* (Thompson & Scott, 1894) which has also been found in sponges (see Schirl, 1973 for review). Detailed examination of the natatory legs, however, reveals several differences in the armatures, notably on the first terminal exopodite segment where *S. elongatus* is II, I + 2, 2 (Sars, 1915: Plate LXVI) and *S stocki* is II, 2, 2; correspondingly the second exopodites are respectively II, I, 4 and III, I, 3. *Scottocheres elongatus* has a 17-segmented first antenna (19 here). *Scottocheres lauberi* Stock, 1967, another sponge dweller is distinguished by the armature of the second, third and fourth exopodites.

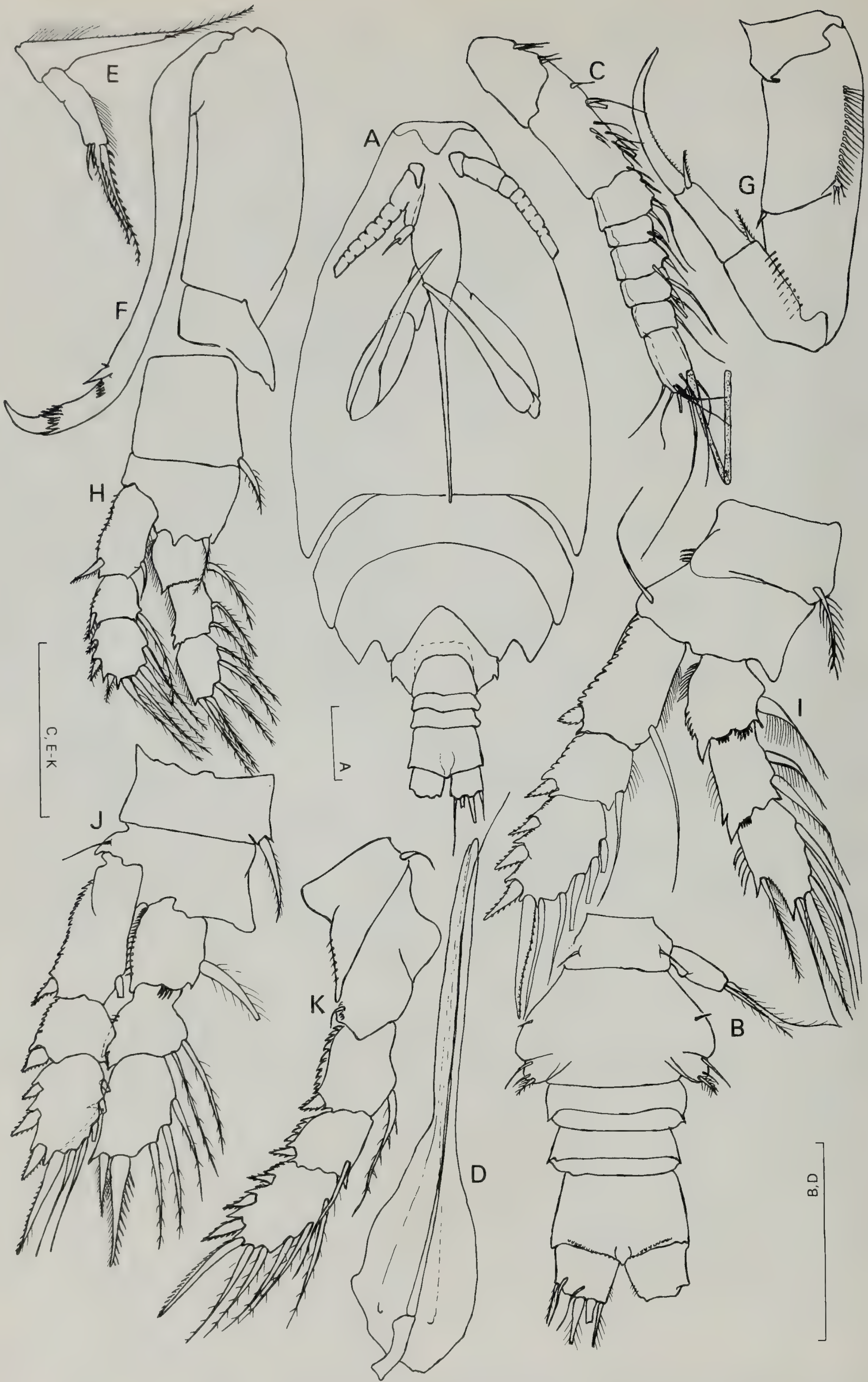

Fig. 11 *Cryptopontius ricinius* n. sp. ♀, holotype. A. Adult, ventral view; B. Urosome, dorsal view; C. First antenna; D. Siphon; E. First maxilla; F. Second maxilla; G. Maxilliped; H. First leg; I. Second leg; J. Third leg; K. Fourth leg. Scale bars = 0.1mm.

Family **DYSPONTIIDAE** Thorell

Cryptopontius ricinius *n. sp.*

Fig. 11 A–K

MATERIAL EXAMINED. Holotype ♀ from the sponge *Ricinia* sp. collected at a depth of 15m at Chik Chau on 6 April 1986. BM(NH) registration number 1989.251.

ETYMOLOGY. This species is named after the sponge in which it was discovered.

FEMALE. Slender, prosome elongate oval, laterally extended into epimeral plates, these being postero–laterally pointed, 0.94mm long (Fig. 11A). Prosome 3.7 times as long as urosome, measuring urosome from posterior border of prosome (genital segment much recessed under posterior border); head 1.3 times as long as wide; rostrum small, produced postero-ventrally; relative lengths of prosome segments 69: 9: 12: 10, head fused to following segment; relative lengths of urosome segments ?: 34: 13: 13: 25: 15 (first segment damaged in dissection). Genital segment expanded posteriorly into 2 pairs of small lobes, outer with long spinule, inner with shorter spinules; 0.7 times as long as wide (Fig. 11B). Caudal rami 0.8 times as long as wide, roughly rectangular; armature 4 terminal elements of varying length, 2 dorsal setules.

First antenna 8-segmented (Fig. 11C); relative lengths 17: 24: 9: 5: 9: 7: 9: 20; armature I–4; II–12; III–4; IV–1+I; V–2; VI–3; VII–1; VIII–8+ae, spine on fourth segment robust. Second antenna lost in dissection. Siphon tubiform, elongate and slender, extending to level of second natatory leg (Fig. 11D). Mandibular stylet 2-segmented, distal segment elongate (Fig. 11D); palp absent. Outer lobe of first maxilla 2-segmented, distal segment with 4 terminal spines, 2 large and spinose, 2 small and unarmed (Fig. 11E); inner lobe single-segmented, longer than outer lobe and tapering distally, with terminal pinnate seta and spinule, segment with internal row of setules, long proximally, shorter distally. Second maxilla 3-segmented, proximal 2 unarmed; distal segment produced into long, curved claw with sub-terminal clusters of spinules (Fig. 11F). Maxilliped 5-segmented (Fig. 11G); segment 2 with lateral rows of setules and internal spine, segments 3 and 4 with internal pinnate spines; terminal segment produced as curved claw, inner concave surface spinulose.

Fourth natatory leg lacking endopodite. Outer surfaces of second, third and fourth legs dentate. Fifth leg cylindrical, single-segmented, about twice as long as wide, with 2 small terminal setae (Fig. 11B).

Armature of natatory legs (Fig. 11 H–K):

	Coxa	Basis	Endopodite	Exopodite
Leg 1	0–I	0–I	0–1; 0–2; 0,2,3	I–1; I–1; III,2,2
Leg 2	0–1	1–0	0–1; 0–2; 1,I+1,3	I–1; I–1; III,I,5
Leg 3	0–1	1–0	0–1; 0–2; 1,II,3	I–1; I–1; III,I,5
Leg 4	0–1	1–0		I–1; I–1; III,I,5

REMARKS. This species was assigned to the genus *Cryptopontius* Giesbrecht, 1899 on the basis of the siphon length, the reduction of the mandible and fourth natatory leg. Leg armature and size separate this from the otherwise similar *C. minor* Stock, 1965. The fifth leg is comparatively long, as found in *C. longipes* Nicholls, 1944, however *C. longipes* has a 9-segmented first antenna in the female and the genital segment is more laterally dilated.

ACKNOWLEDGEMENTS. I am grateful to Dr Geoffrey Boxshall for his help and advice on the preparation of the text and to the Trustees of the Natural History Museum in London for the use of Museum facilities for this piece of research.

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The freshwater cyclopoid copepods of Nigeria, with an illustrated key to all species

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INTRODUCTION

Dracunculiasis is caused by the guineaworm, *Dracunculus medinensis* L., and is endemic in parts of Africa and Asia. The vectors of guineaworm are cyclopoid copepods that inhabit stagnant ponds and the disease is especially prevalent in rural areas among people who obtain their drinking water from such ponds. The vectors are commonly referred to as '*Cyclops*' but *D. medinensis* exhibits a high level of host specificity and only a few species act as vectors in nature. *Mesocyclops leuckarti* (Claus) is widely reported as the common intermediate host in India (Sarkar, 1982) and Africa (Onabamiro, 1950; Muller, 1970). Other reported hosts include species of the genera *Mesocyclops* Sars (Sarkar, 1982), *Thermocyclops* Kiefer (Onabamiro, 1952*a*) and *Metacyclops* Kiefer (Steib, 1985). The correct identification of the copepod intermediate hosts is important in mapping the geographical distribution and spread of the disease, and is vital in the development of eradication programs which aim to combat the disease by control of the vectors.

Recent progress in copepod systematics has refined the level of taxonomic resolution of these freshwater copepods and it is now known that *Mesocyclops leuckarti* does not occur in either Africa or India (Kiefer, 1981; Van de Velde, 1984). There is, therefore, an obvious need to record these taxonomic changes, to review earlier records, and to update the nomenclature of the host wherever possible. The purpose of the present paper is to review all records of freshwater cyclopoid copepods from Nigeria, including those that act as vectors of guineaworm, and to give their current names.

THE FRESHWATER CYCLOPOID COPEPODS OF NIGERIA

A. Valid species

Family Cyclopidae
Subfamily Halicyclopinae

1. *Halicyclops korodiensis* Onabamiro, 1952: (Figs. 1–3)

This species was described from a brackish pool near the Lagoon at Ikorodu, 16 miles from Lagos, South West Nigeria (Onabamiro, 1952*a*). It was redescribed by Gabriel et al. (1987) from material collected in the estuary of the Warri River, Nigeria. It has since been recorded from the estuary of the river Bonny near Port Harcourt (unpublished data).

MATERIAL EXAMINED. 4♀♀ syntypes collected from brackish pool near the lagoon at Ikorudu, near Lagos, Nigeria by Onabamiro, BM(NH) Reg.No. 1952.11.28.7–8. Additional material, 3♀♀, 5♂♂ and 3 copepodids collected from estuary of River Bonny near Port Harcourt by Mrs E. Etta, BM(NH) Reg. No. 1985.108.

2. *Halicyclops pondoensis* Wooldridge, 1977: (Figs. 4–6)

This species was described from the plankton in the Msikaba and Mbotyi estuaries on the Pondoland coast, Transkei (Wooldridge, 1977). It has since been recorded in the estuary of the Bonny river near Port Harcourt (unpublished data).

MATERIAL EXAMINED. 6♀♀, 1♂ and 9 copepodids collected from estuary of River Bonny near Port Harcourt by Mrs E. Etta, BM(NH) Reg. Nos. 1985.258–273.

Subfamily Eucyclopinae

3. *Macrocyclops albidus oligolasius* Kiefer, 1928: (Fig. 7)

This species was first recorded from Nigeria by Onabamiro (1952*a*) under the name *Macrocylops oligolasius*. Green (1962) reported this subspecies from the river Sokoto.

MATERIAL EXAMINED. 1♀ collected from South West Nigeria by Onabamiro, BM(NH) Reg. No. 1957.2.15.6.

4. *Eucyclops serrulatus* (Fischer, 1851): (Figs. 18, 25)

This species was recorded from South West Nigeria by Onabamiro (1952*a*) under the name *Eucyclops agilis* (Koch). Green (1962) reported it from the river Sokoto. The material recorded as *E. productus* Kiefer by Onabamiro (1952*b*) is indistinguishable from *E. serrulatus* collected in the same area.

MATERIAL EXAMINED. 5♀♀ collected from South West Nigeria by Onabamiro, BM(NH) Reg. No. 1957.2.15.11. Numerous specimens collected from Mkpani village, Cross River State, Nigeria by Braide. 1♀ from South West Nigeria, reported as *E. productus* by Onabamiro (1952*b*), BM(NH) Reg. No. 1957.2.15.10.

5. *Eucyclops macruroides* (Lilljeborg, 1901): (Fig. 20)

This species was recorded from South West Nigeria by Onabamiro (1952*a*).

MATERIAL EXAMINED. Nigerian specimens of this species were not available: 2♀♀ collected by J. P. Harding in Wise Een Tarn, Westmorland, England, BM(NH) Reg. No. 1964.4.2.6.

6. *Eucyclops agiloides* (Sars, 1909): (Figs. 22, 23–4)

This species has a wide distribution in Africa and was recorded from Nigeria by Onabamiro (1952*b*).

MATERIAL EXAMINED 10♀♀ collected from South West Nigeria by Onabamiro, BM(NH) Reg. No. 1957.2.15.9.

7. *Afrocyclops gibsoni* (Brady, 1904): (Figs. 19, 26b-28)

This species was recorded as *Eucyclops* (*Afrocyclops*) *gibsoni* by Onabamiro (1951) from South West Nigeria and as *A.gibsoni* in 1952. It was reported from the Sokoto river by Green (1962) and from Oyo State by Sridhar & Kale (1985). The *Cyclops longistylis* reported from northern Nigeria by Brady (1910) were regarded by Lindberg (1950) as probably belonging to *Afrocyclops gibsoni*.

MATERIAL EXAMINED. 2♀♀ collected from South West Nigeria by Onabamiro, BM(NH) Reg. No. 1957.2.15.8.

8. *Afrocyclops curticornis* (Kiefer, 1932): (Fig. 26a)

This species was recorded from South West Nigeria by Onabamiro (1952*a*).

MATERIAL EXAMINED. None.

9. *Afrocyclops doryphorus* (Kiefer, 1935): (Figs. 31–32)

This species was recorded from South West Nigeria by Onabamiro (1952*b*).

MATERIAL EXAMINED. 1♀ collected from South West Nigeria by Onabamiro, BM(NH) Reg. No. 1957.2.15.7.

10. *Afrocyclops ikennus* Onabamiro, 1957: (Figs. 29–30)

This species was described from material taken at Ikenne in South West Nigeria (Onabamiro, 1957).

MATERIAL EXAMINED. Paratype ♀ collected on 24 May 1951 by Onabamiro (1957) at Ikenne, Ijebu-Remo, Nigeria, BM(NH) Reg. No. 1957.2.15.5.

11. *Tropocyclops prasinus* (Fischer, 1860): (Fig. 17)

This species was recorded by Sridhar & Kale (1985) from Oyo State. The *Cyclops virescens* reported from Nigeria by Brady (1910) is treated as a synonym of *T. prasinus* by Dussart & Defaye (1985).

MATERIAL EXAMINED. Nigerian specimens of this species were not available: 2♀♀ collected in Egypt, BM(NH) Reg. Nos. 1939.3.15.31–33 and several ♀♀ collected in Kirkudbright, Scotland, BM(NH) Reg. Nos. 1911.11.8.41160–41179.

12. *Tropocyclops prasinus shagamiensis* Onabamiro, 1957

This subspecies was described from material collected in stagnant side pools formed by the Ibu river at Shagamu, and in similar habitats at Ilaro and Ijebu in South West Nigeria (Onabamiro, 1957).

MATERIAL EXAMINED. Paratype ♀ collected on 10 April 1951 from stagnant side pools formed by Ibu River at Shagamu, Nigeria, BM(NH) Reg. No. 1957.2.15.4.

13. *Tropocyclops confinis* (Kiefer, 1930): (Figs. 14, 21)

This species was recorded from South West Nigeria by Onabamiro (1951, 1952*a*). Lindberg (1951) recorded *T.confinis* from the Okolom area of Nigeria. The *Cyclops virescens* reported from Nigeria by Brady (1910) were regarded as probably identical with *Tropocyclops confinis* by Lindberg (1950, and in Onabamiro, 1952*a*), although Dussart & Defaye (1985) treat *C.virescens* as as synonym of *Tropocyclops prasinus*.

MATERIAL EXAMINED 1♀ collected from South West Nigeria by Onabamiro, BM(NH) Reg. No. 1957.2.15.12. Numerous specimens collected from Mkpani village, Cross River State, Nigeria by Braide.

14. *Tropocyclops confinis awiensis* Onabamiro 1957

This subspecies was described from material collected from large pools in the shrinking bed of the river Omi-Awa, 30 miles south of Ibadan (Onabamiro, 1957).

MATERIAL EXAMINED. Paratype ♀ collected from River Omi-Awa, Nigeria by Onabamiro, BM(NH) Reg. No. 1957.2.15.3.

15. *Tropocyclops onabamiroi* Lindberg, 1950: (Fig. 15)

This species was described on material collected by Onabamiro from South West Nigeria (Lindberg, 1950). It was also reported from Oyo State by Sridhar & Kale (1985).

MATERIAL EXAMINED. 1♀ collected from South West Nigeria by Onabamiro, BM(NH) Reg. No. 1957.2.15.13.

16. *Tropocyclops mellanbyi* Onabamiro, 1952: (Fig. 16)

This species was described as widespread within Nigeria by Onabamiro (1952*a*) who recorded it from Ibadan, Kajola, and Sagamu (Ijebu province). It was suggested as a possible synonym of *Tropocyclops prasinus prasinus* by Lindberg (1955) and treated as incertae sedis by Dussart & Defaye (1985).

MATERIAL EXAMINED. Paratype ♀♀ collected on 7 March 1950 by Onabamiro (1952*a*) from reservoir near Ibadan, Nigeria, BM(NH) Reg. No. 1952.11.28.3–4.

17. *Paracyclops affinis* (Sars, 1863): (Figs. 8–9)

This species is widely distributed in Africa and was reported from Nigeria by Onabamiro (1952*b*).

MATERIAL EXAMINED. Numerous specimens collected from Mkpani village, Cross River State, Nigeria by Braide; 1♀ collected by R.Gurney from Calthorpe, England, BM(NH) Reg. No. 1950.9.20.193.

18. *Ectocyclops phaleratus* (Koch, 1838): (Figs. 10–11)

This species was recorded from South West Nigeria as *Platycyclops phaleratus* by Onabamiro in 1951 and as *Ectocyclops phaleratus* in 1952. A specimen of *E.phaleratus* sensu lato was reported from the river Sokoto by Green (1962).

MATERIAL EXAMINED. 1♀ collected from South West Nigeria by Onabamiro, BM(NH) Reg. No. 1957.2.15.14.

19. *Ectocyclops phaleratus ilariensis* Onabamiro, 1952: (Fig. 13)

This subspecies was described as a new species, *E.ilariensis*, on material collected near Ilaro in South West Nigeria by Onabamiro (1952*a*). It was treated as a subspecies by Dussart & Defaye (1985).

MATERIAL EXAMINED Paratype ♀♀ collected by Onabamiro (1952*a*) on 18 October 1950 at Ilaro, Nigeria, BM(NH) Reg. Nos. 1952.11.28.5–6.

20. *Ectocyclops compactus* (Sars, 1909): (Fig. 12)

This species was reported from the river Sokoto by Green (1962).

MATERIAL EXAMINED. Nigerian specimens of this species were not available: 1♀ collected by C. K. Richards & R. J. Owen in Lake Young, East Africa, BM(NH) Reg. No. 1941.5.16.101.

Subfamily Cyclopinae

21. *Metacyclops pseudoanceps* (Green, 1962): (Fig. 33–34)

This species was described as a new species of *Microcyclops* by Green (1962) from material collected in the Sokoto river. It was regarded as belonging to the genus *Metacyclops* by Dussart & Defaye (1985).

MATERIAL EXAMINED. 2♀♀ syntypes donated by Prof. J. Green, collected in the Sokoto river, BM(NH) Reg. Nos. 1989.964–965.

22. *Metacyclops minutus* (Claus, 1863): (Fig. 35)

This species was recorded from Nigeria by Onabamiro (1952*b*) under the name *Microcyclops minutus*.

MATERIAL EXAMINED. 1♀ collected from South West Nigeria by Onabamiro, BM(NH) Reg. No. 1957.2.15.17.

23. *Microcyclops varicans* (Sars, 1863): (Fig. 36)

This species was recorded from South West Nigeria by Onabamiro (1952*a*), from the river Sokoto by Green (1962) and from Ijere, in Oyo State by Sridhar & Kale (1985). It was recorded from northern Nigeria by Gurney (1933) as *Cyclops* (*Microcyclops*) *varicans*.

MATERIAL EXAMINED. 1♀ (damaged with caudal rami missing) collected from South West Nigeria by Onabamiro, BM(NH) Reg. No. 1957.2.15.17, and 1♀ as *M. varicans subaequalis* from same region, BM(NH) Reg. No. 1957.2.15.16.

24. *Microcyclops jenkinae* Lowndes, 1933: (Figs. 37–39)

This species was reported from South West Nigeria by Onabamiro (1951, 1952*a*) as *Cryptocyclops jenkinae*.

MATERIAL EXAMINED. 1♂ collected by Dr E. I. Braide at Okpuru Udebe, Anambra, Nigeria.

25. *Cryptocyclops bicolor* (Sars, 1863): (Fig. 40)

Brady (1910) first recorded this species from Nigeria, as *Cyclops bicolor*. His species was regarded as probably identical to *Cryptocyclops linjanticus* (Kiefer) by Lindberg (in Onabamiro, 1952*a*). Dussart & Defaye (1985) list this species as occurring in Nigeria, based on Brady's record. Its presence in Nigeria requires confirmation.

MATERIAL EXAMINED. Nigerian specimens of this species were not available: 1♀ collected from Lake Naivasha, Kenya, BM(NH) Reg. No. 1933.9.25.20.

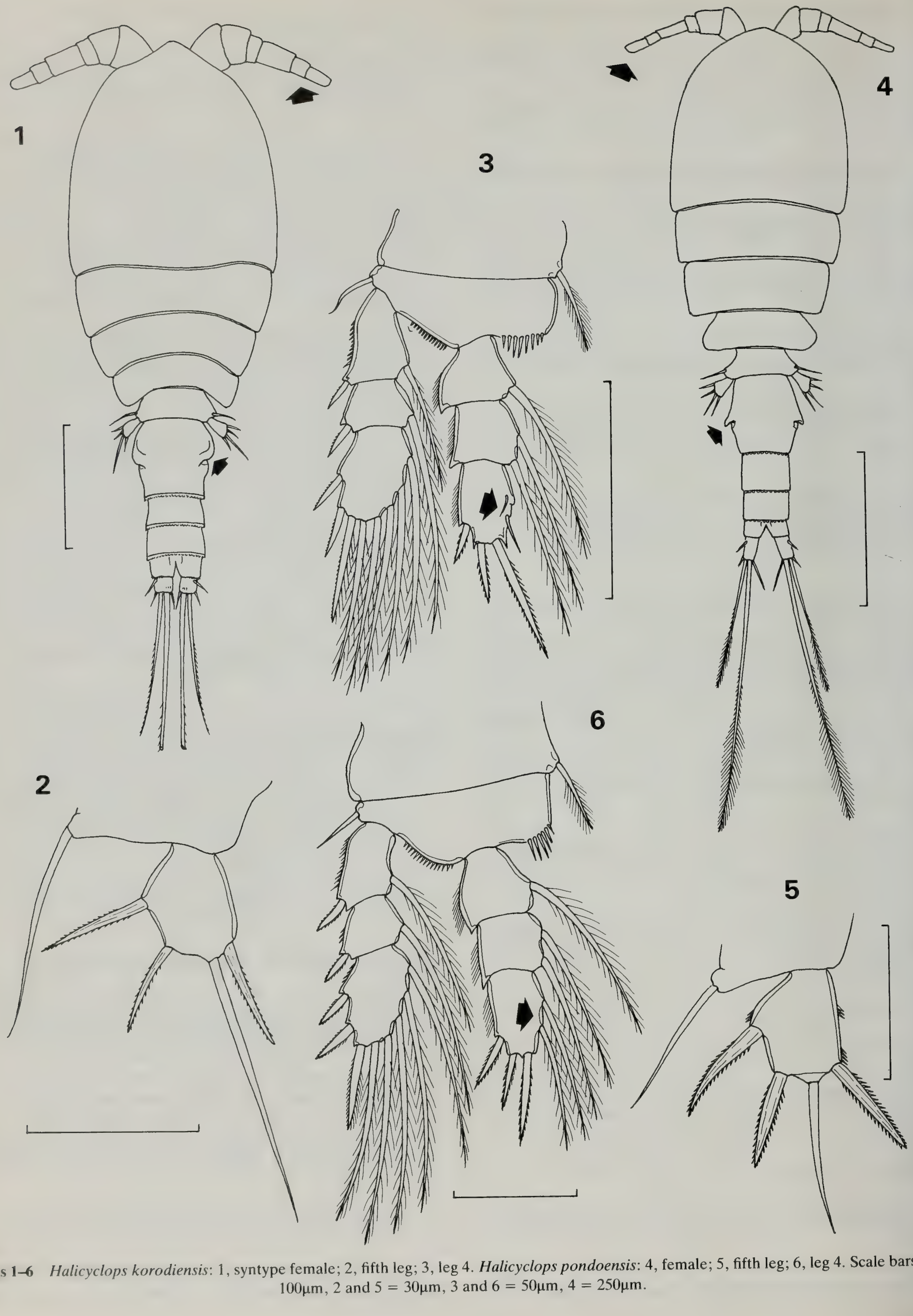
26. *Cryptocyclops linjanticus* (Kiefer, 1928): (Figs. 41–42)

This species was recorded in South West Nigeria as *Microcyclops linjanticus* by Onabamiro (1951, 1952a). It was reported from Ijere, Oyo State by Sridhar & Kale (1985).

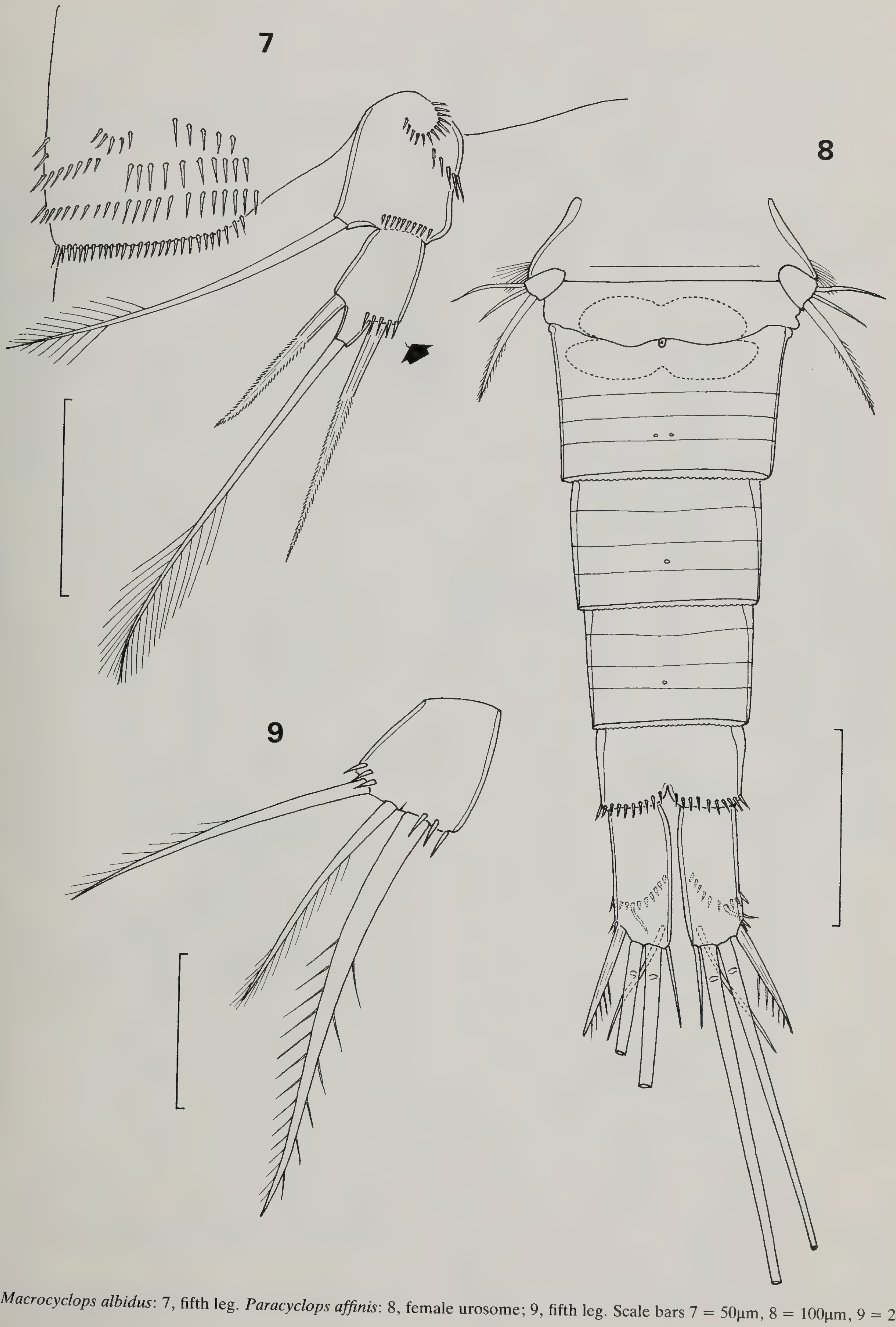
MATERIAL EXAMINED. 2♀♀ collected from South West Nigeria by Onabamiro, BM(NH) Reg. Nos. 1950.8.5.5 and 1957.2.15.15. The *M.linjanticus* collected by Onabamiro and stored as BM(NH) Reg. No. 1950.8.5.6. is a fifth copepodid of *Mesocyclops*; 2♀♀ collected by Dr E. I. Braide from Benue, Nigeria.

27. *Mesocyclops aspericornis* (Daday, 1906): (Figs. 43, 59)

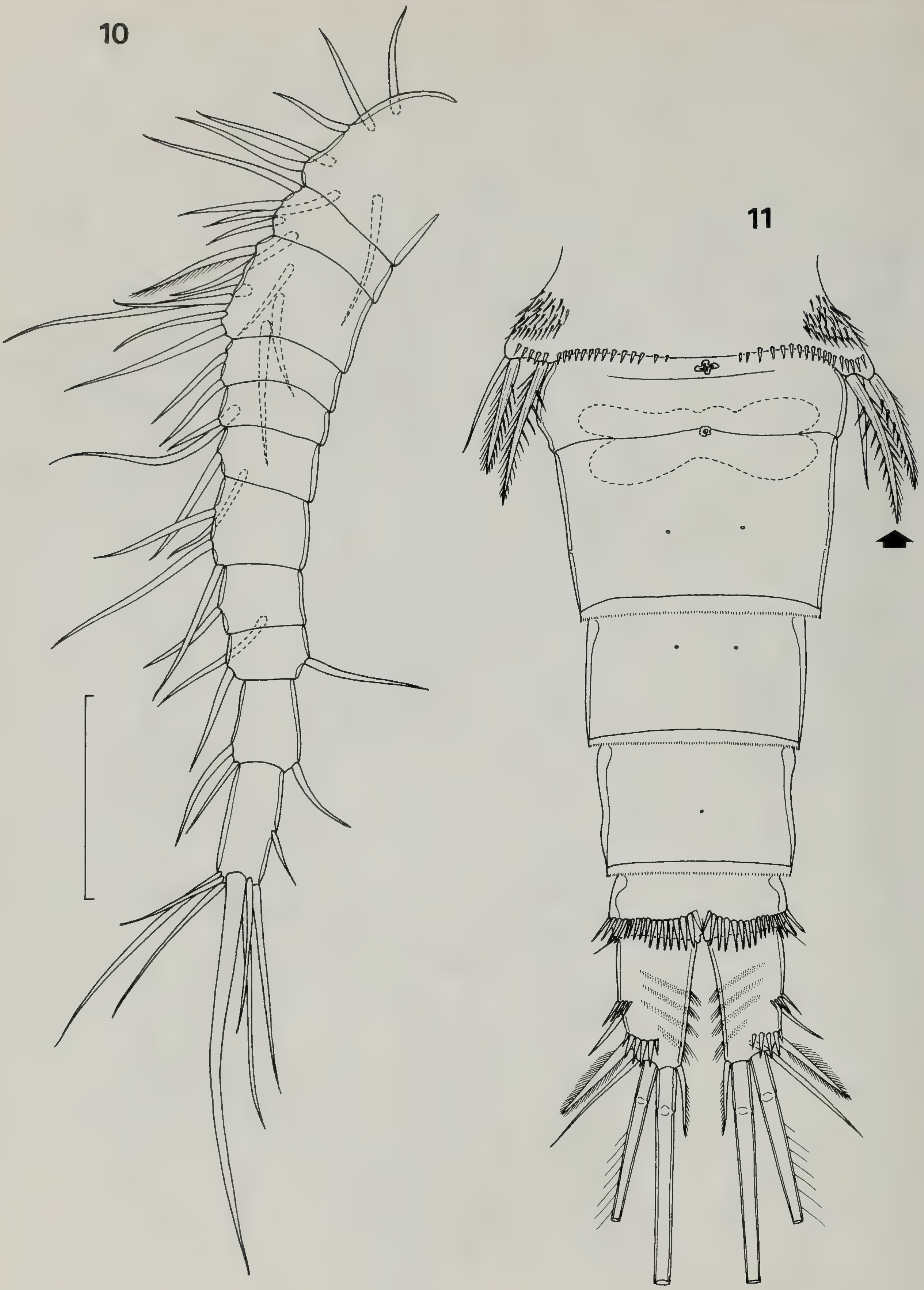
This species is the only *Mesocyclops* species found in Africa that also has a wide distribution in the Oriental region (Van



Figs 1–6 *Halicyclops korodiensis*: 1, syntype female; 2, fifth leg; 3, leg 4. *Halicyclops pondoensis*: 4, female; 5, fifth leg; 6, leg 4. Scale bars 1 = 100µm, 2 and 5 = 30µm, 3 and 6 = 50µm, 4 = 250µm.



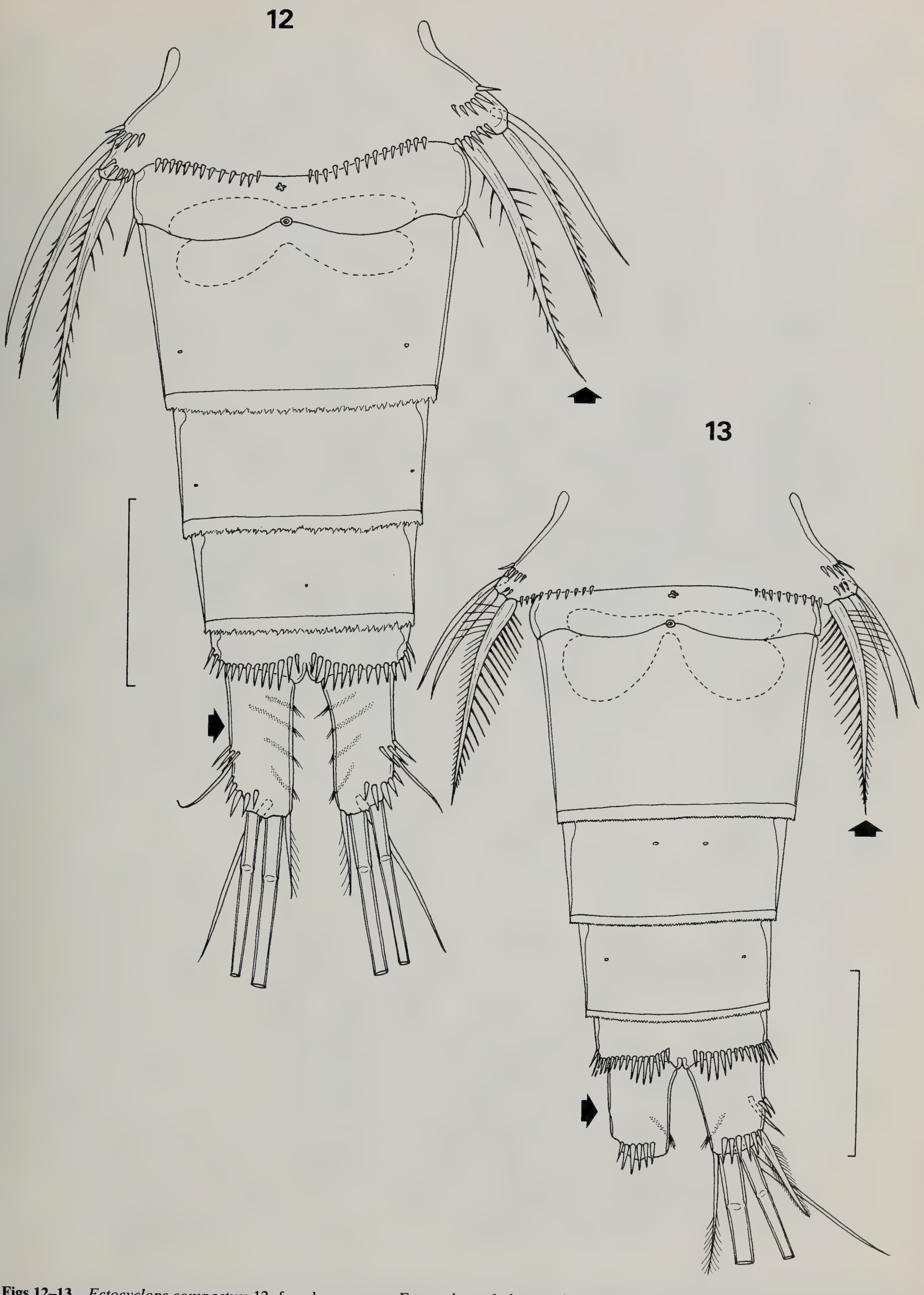
Figs 7–9 *Macrocyclops albidus*: 7, fifth leg. *Paracyclops affinis*: 8, female urosome; 9, fifth leg. Scale bars 7 = 50μm, 8 = 100μm, 9 = 25μm.



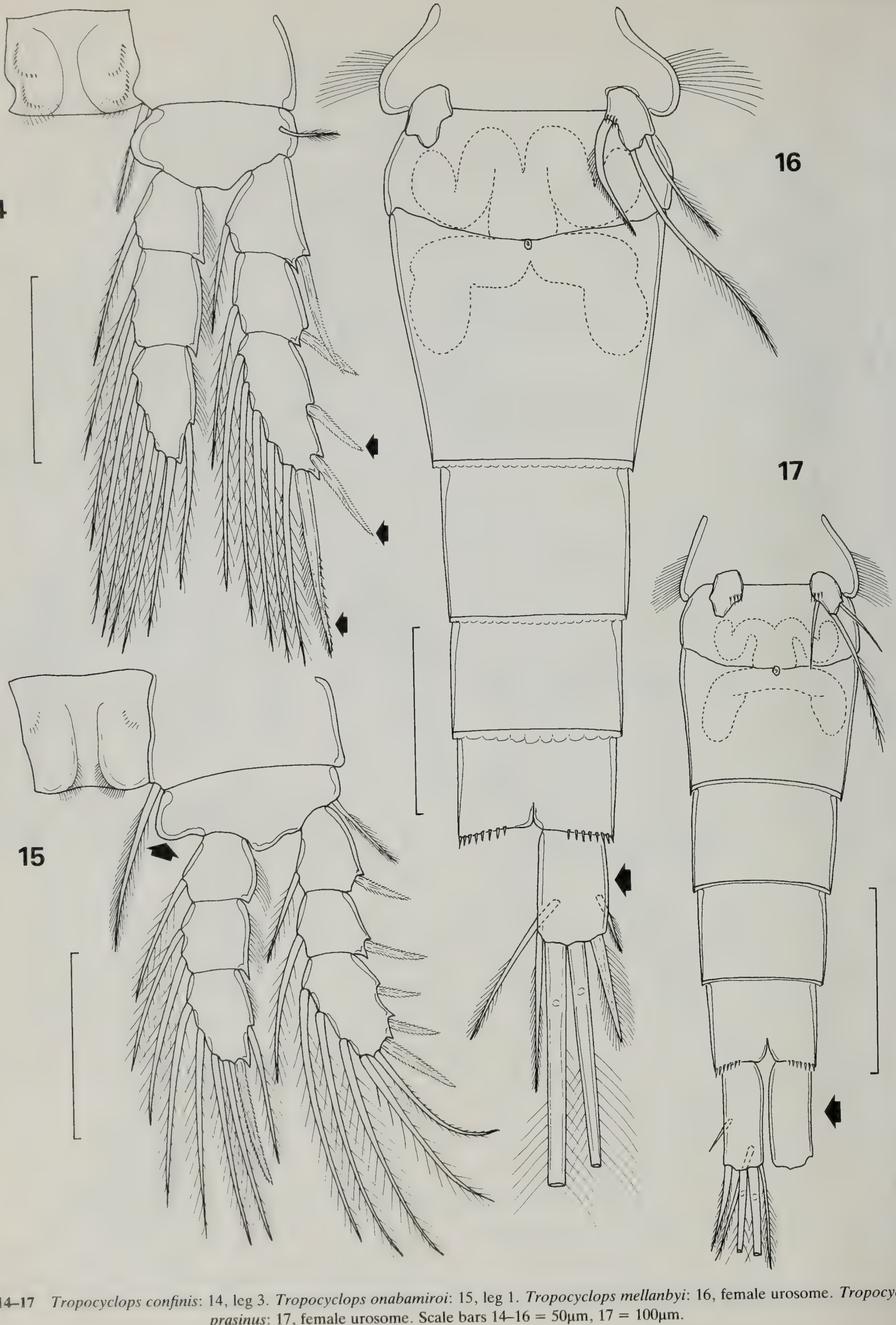
Figs 10–11 *Ectocyclops phaleratus*: 10, female antennule; 11, female urosome. Scale bars 10 = 50µm, 11 = 100µm.

de Velde, 1984). It was identified in material from Okolom, Nigeria by Van de Velde (1984). This material had previously been reported as *Mesocyclops leuckarti* by Lindberg (1951). Jeje (1988) reported *M.aspericornis* from a range of habitats at Ibadan, Benin city, Ilorin, Moniya and Margia, and from the river Bonney and Nike lake.

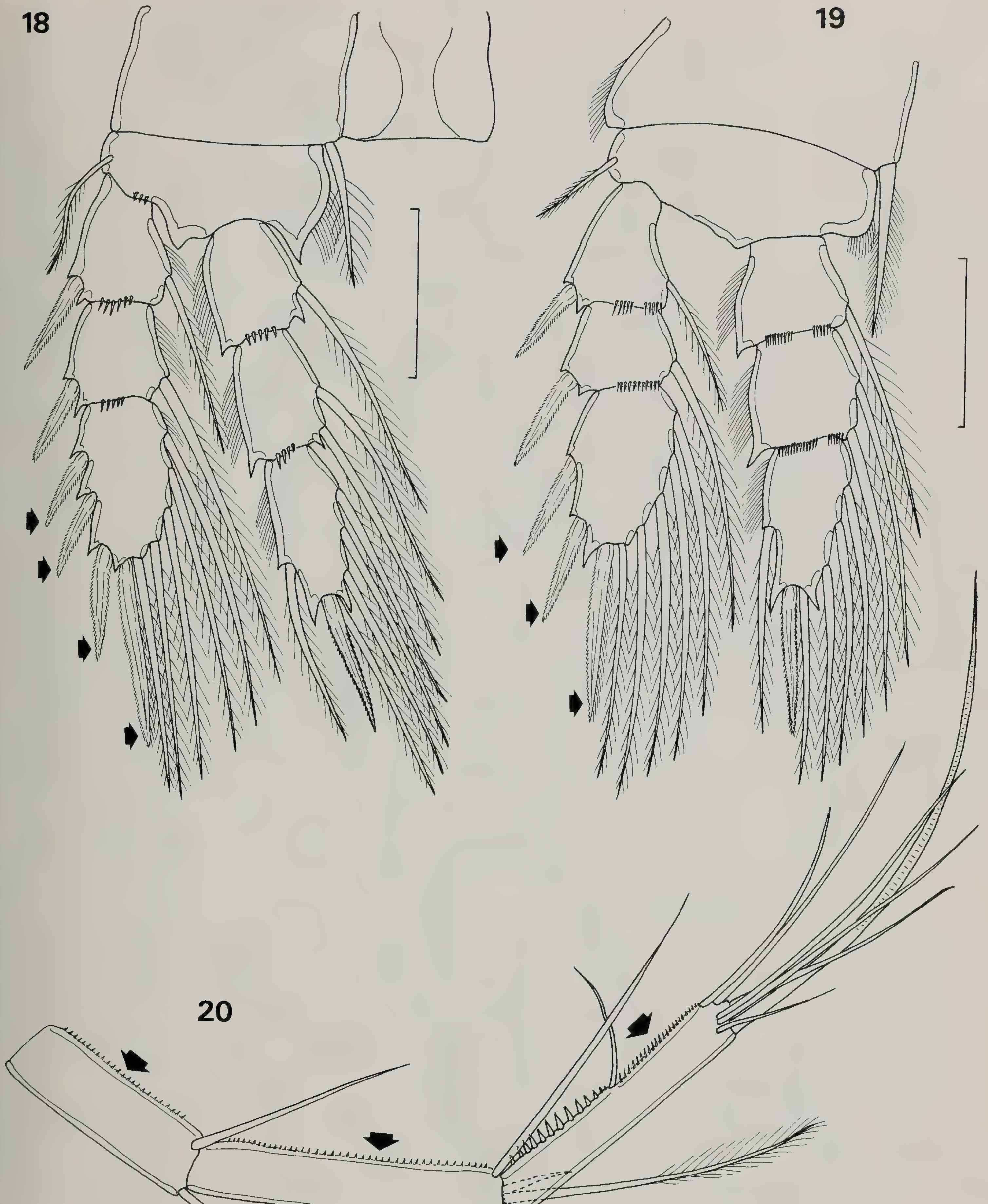
MATERIAL EXAMINED. Numerous specimens collected from



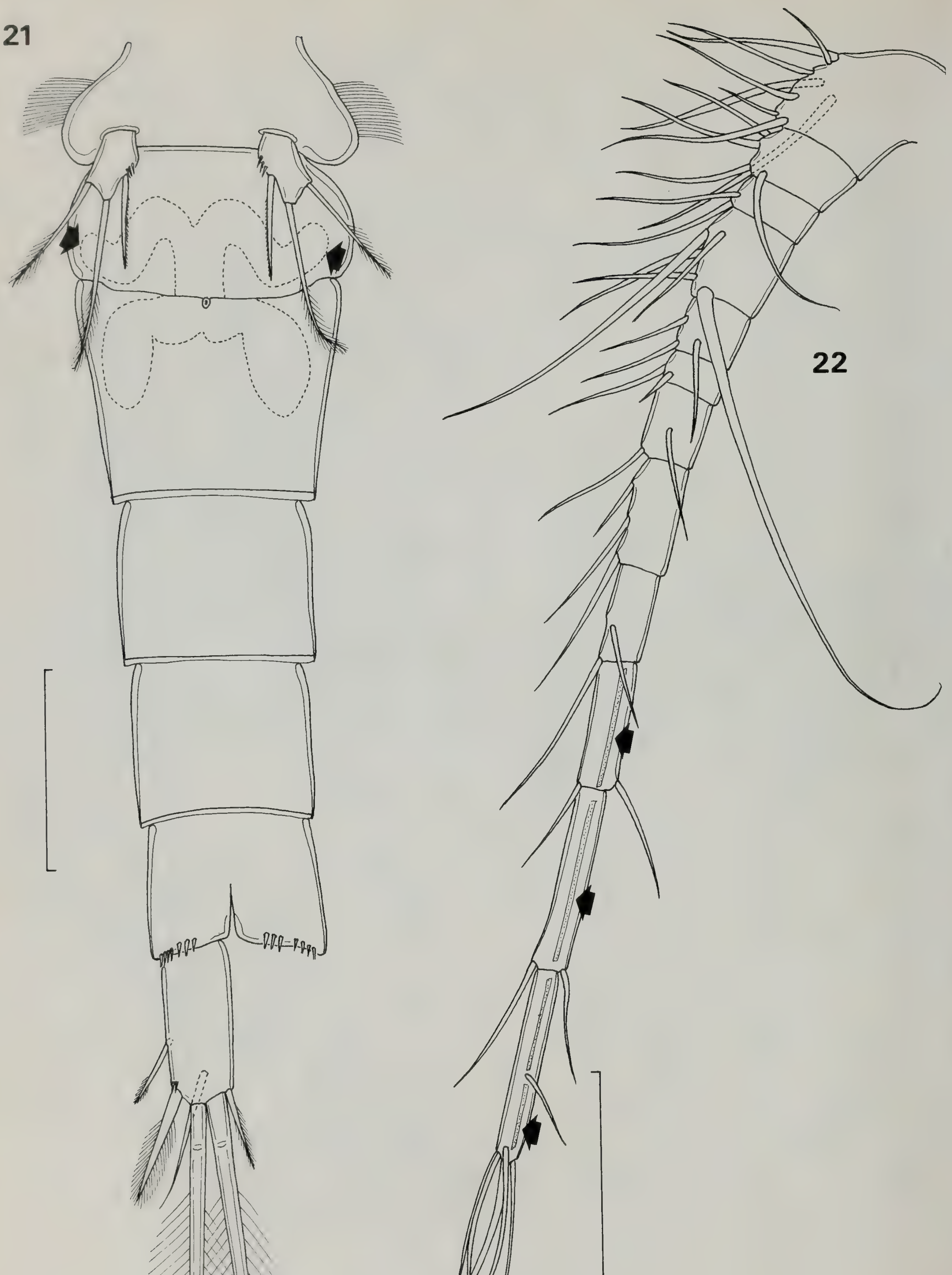
Figs 12–13 *Ectocyclops compactus*: 12, female urosome. *Ectocyclops phaleratus ilariensis*: 13, female urosome. Scale bars = 100μm.



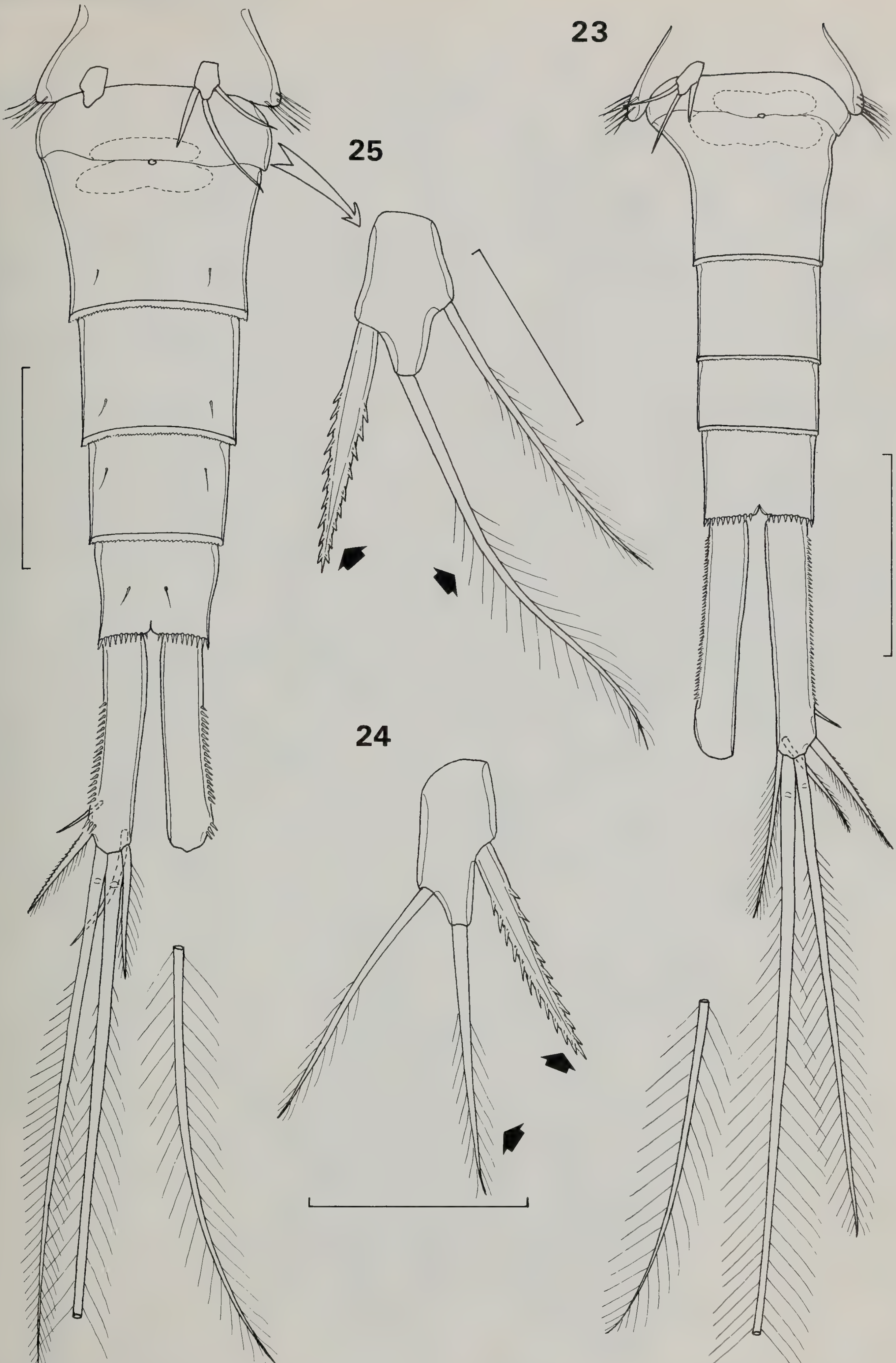
Figs 14–17 *Tropocyclops confinis*: 14, leg 3. *Tropocyclops onabamiroi*: 15, leg 1. *Tropocyclops mellanbyi*: 16, female urosome. *Tropocyclops prasinus*: 17, female urosome. Scale bars 14–16 = 50μm, 17 = 100μm.



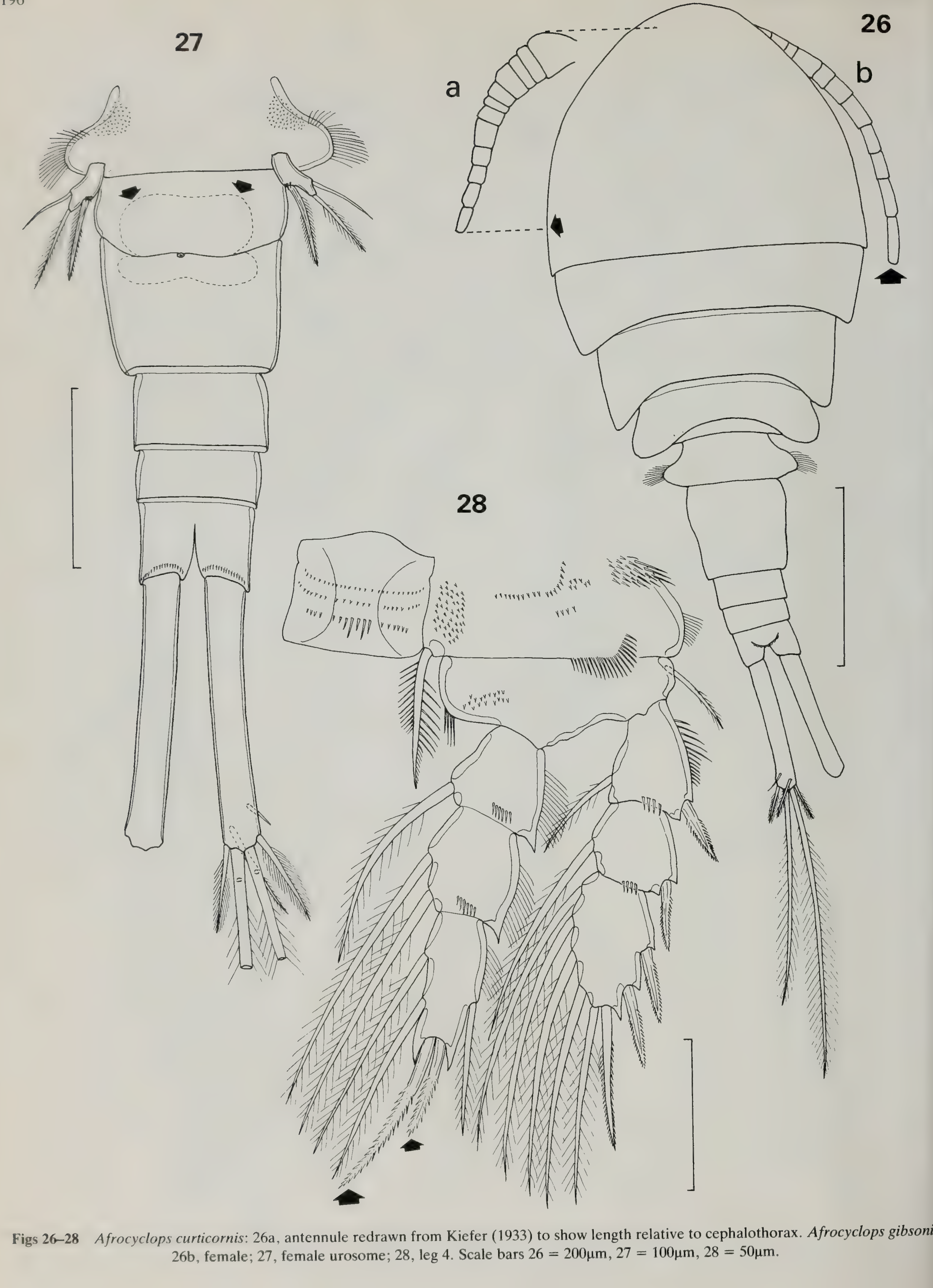
Figs 18–20 *Eucyclops serrulatus*: 18, leg 3; *Afrocyclops gibsoni*: 19, leg 3. *Eucyclops macruroides*: 20, distal 3 segments of female antennule. Scale bars = 50μm.



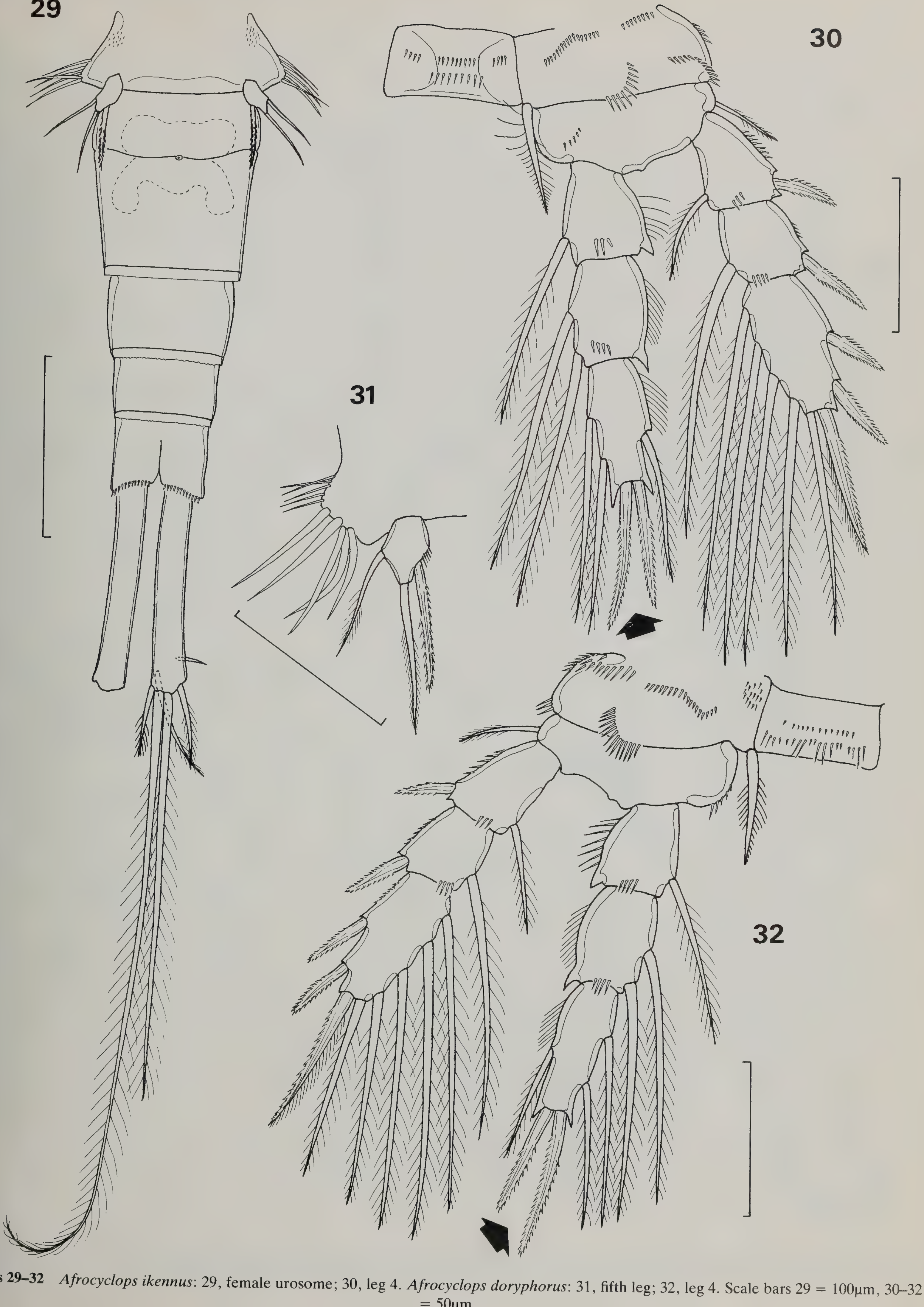
Figs 21–22 *Tropocyclops confinis*: 21, female urosome. *Eucyclops agiloides*: 22, female antennule. Scale bars 21 = 50μm, 22 = 100μm.



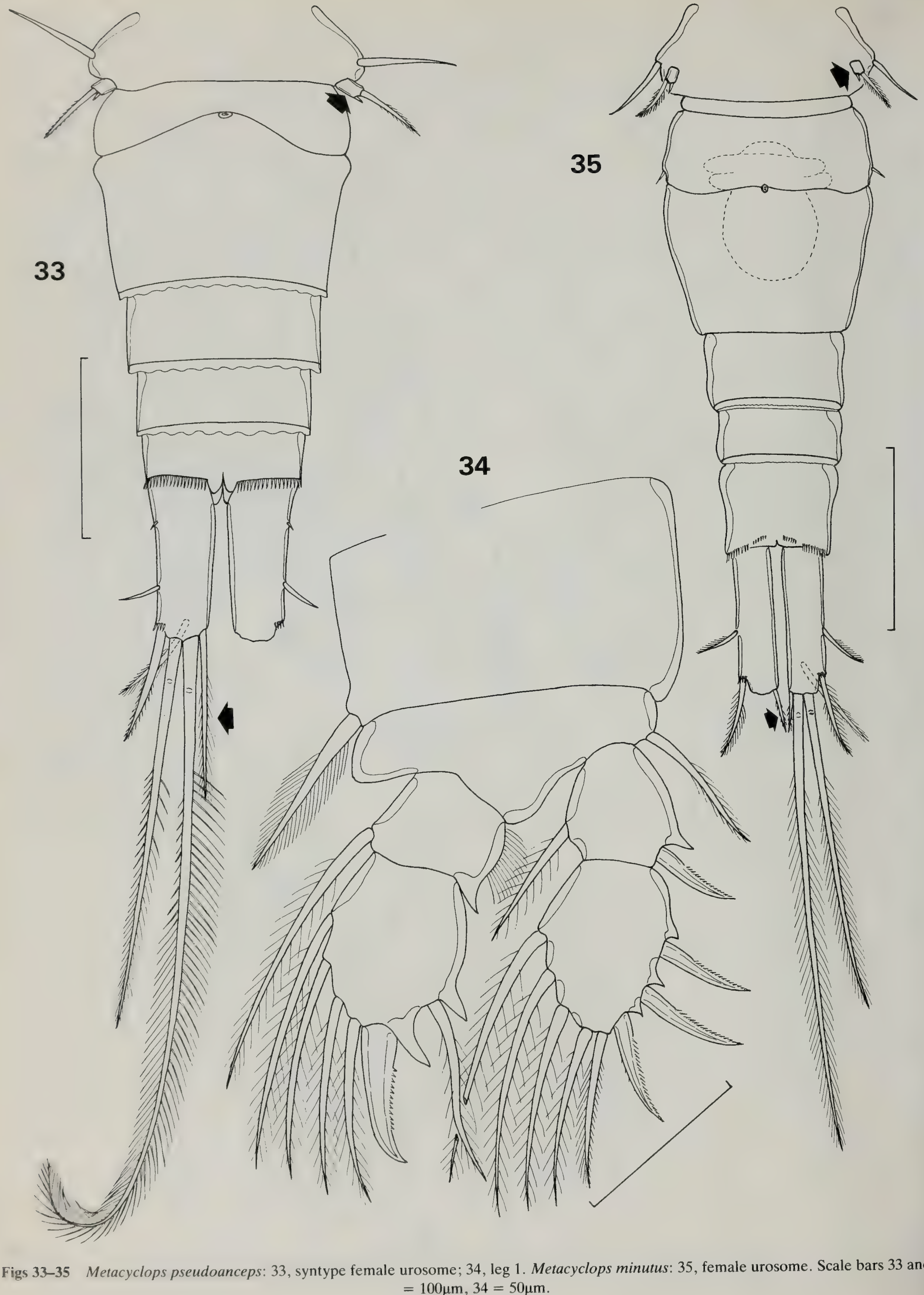
Figs 23–25 *Eucyclops agiloides*: 23, female urosome; 24, fifth leg. *Eucyclops serrulatus*: 25, female urosome, with detail of fifth leg. Scale bars 23 and 25 = 100 μm, 24 = 25μm.



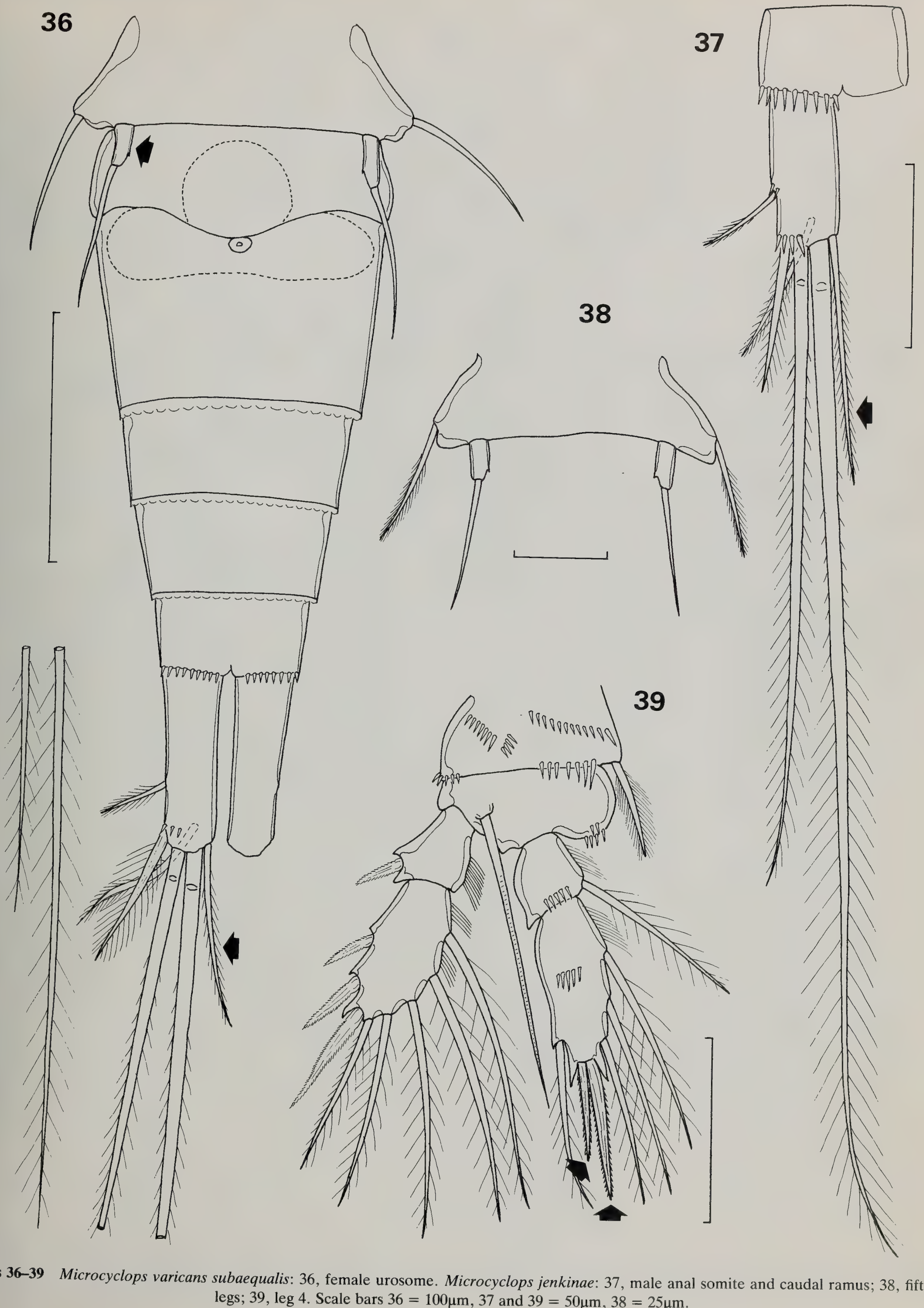
Figs 26–28 *Afrocyclops curticornis*: 26a, antennule redrawn from Kiefer (1933) to show length relative to cephalothorax. *Afrocyclops gibsoni*: 26b, female; 27, female urosome; 28, leg 4. Scale bars 26 = 200µm, 27 = 100µm, 28 = 50µm.



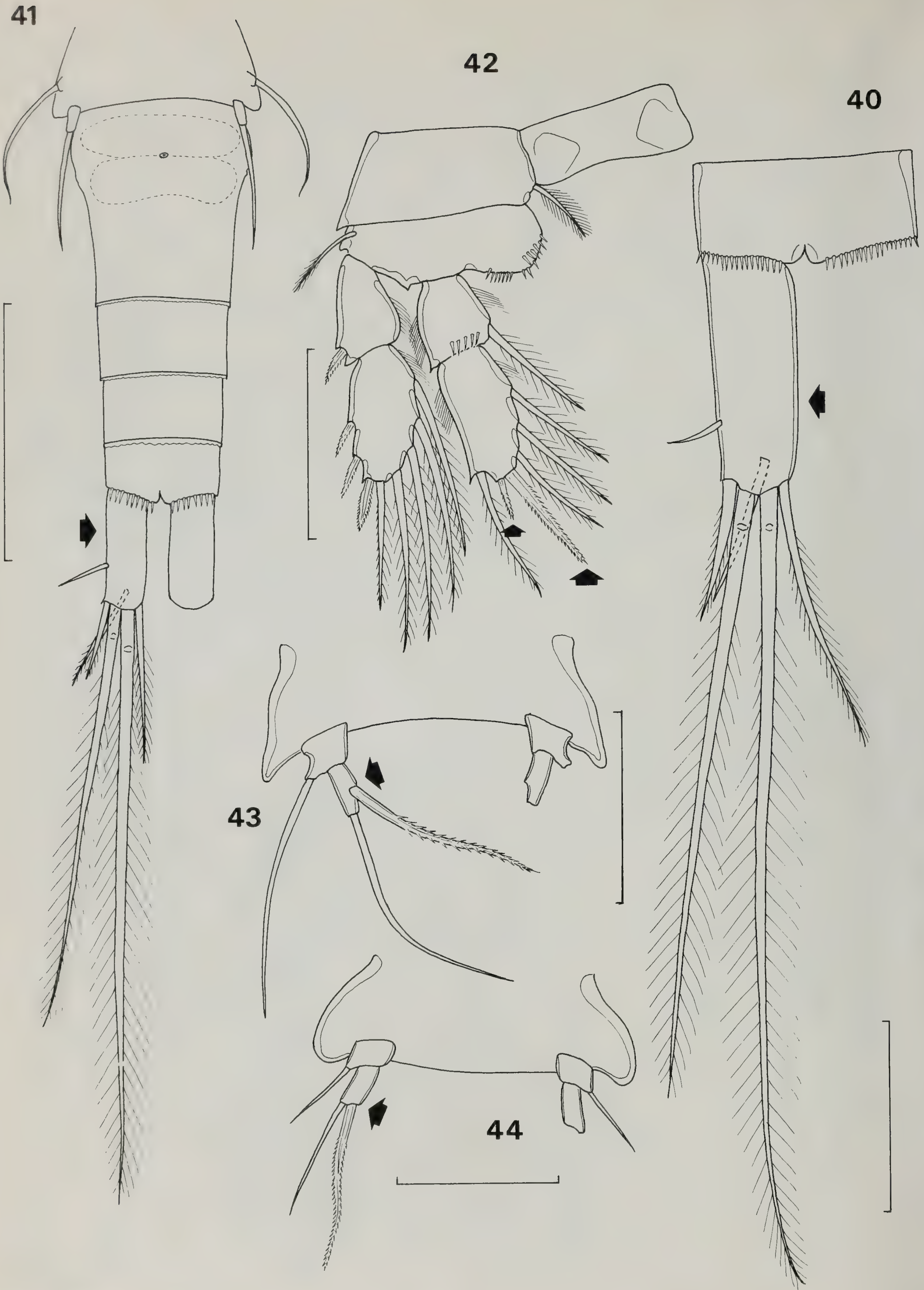
Figs 29–32 *Afrocyclops ikennus*: 29, female urosome; 30, leg 4. *Afrocyclops doryphorus*: 31, fifth leg; 32, leg 4. Scale bars 29 = 100μm, 30–32 = 50μm.



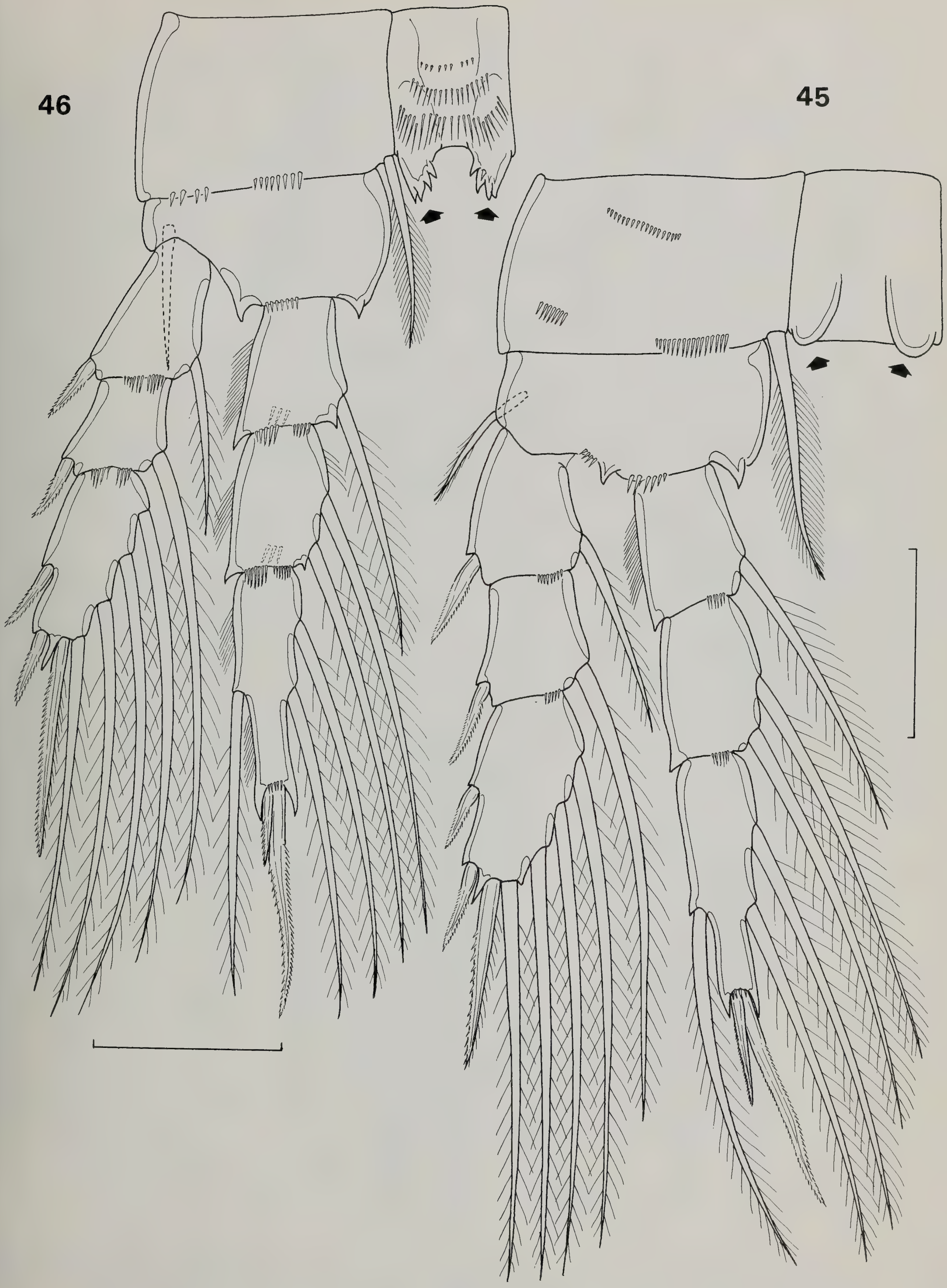
Figs 33–35 *Metacyclops pseudoanceps*: 33, syntype female urosome; 34, leg 1. *Metacyclops minutus*: 35, female urosome. Scale bars 33 and 35 = 100μm, 34 = 50μm.



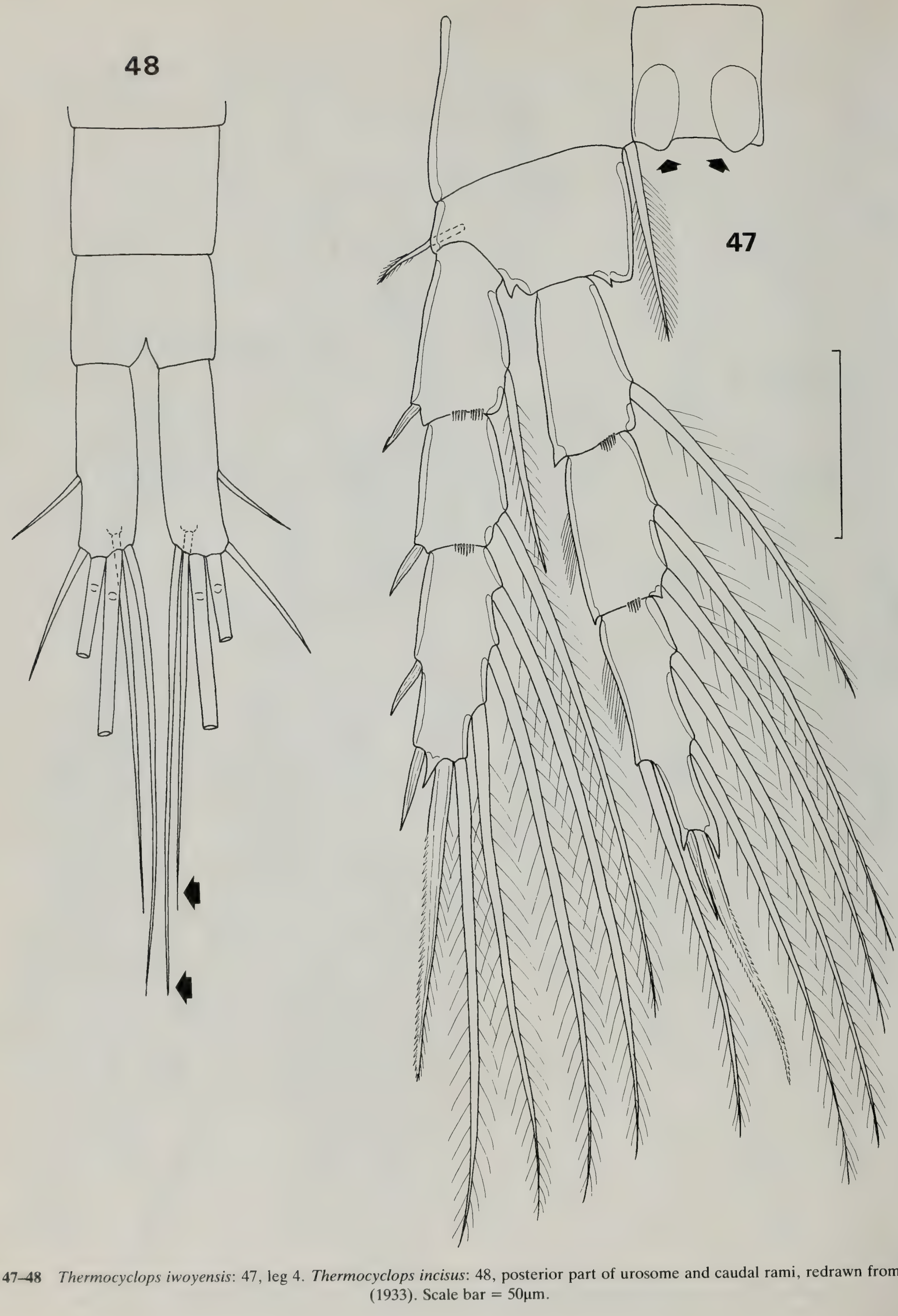
Figs 36–39 *Microcyclops varicans subaequalis*: 36, female urosome. *Microcyclops jenkinae*: 37, male anal somite and caudal ramus; 38, fifth legs; 39, leg 4. Scale bars 36 = 100μm, 37 and 39 = 50μm, 38 = 25μm.



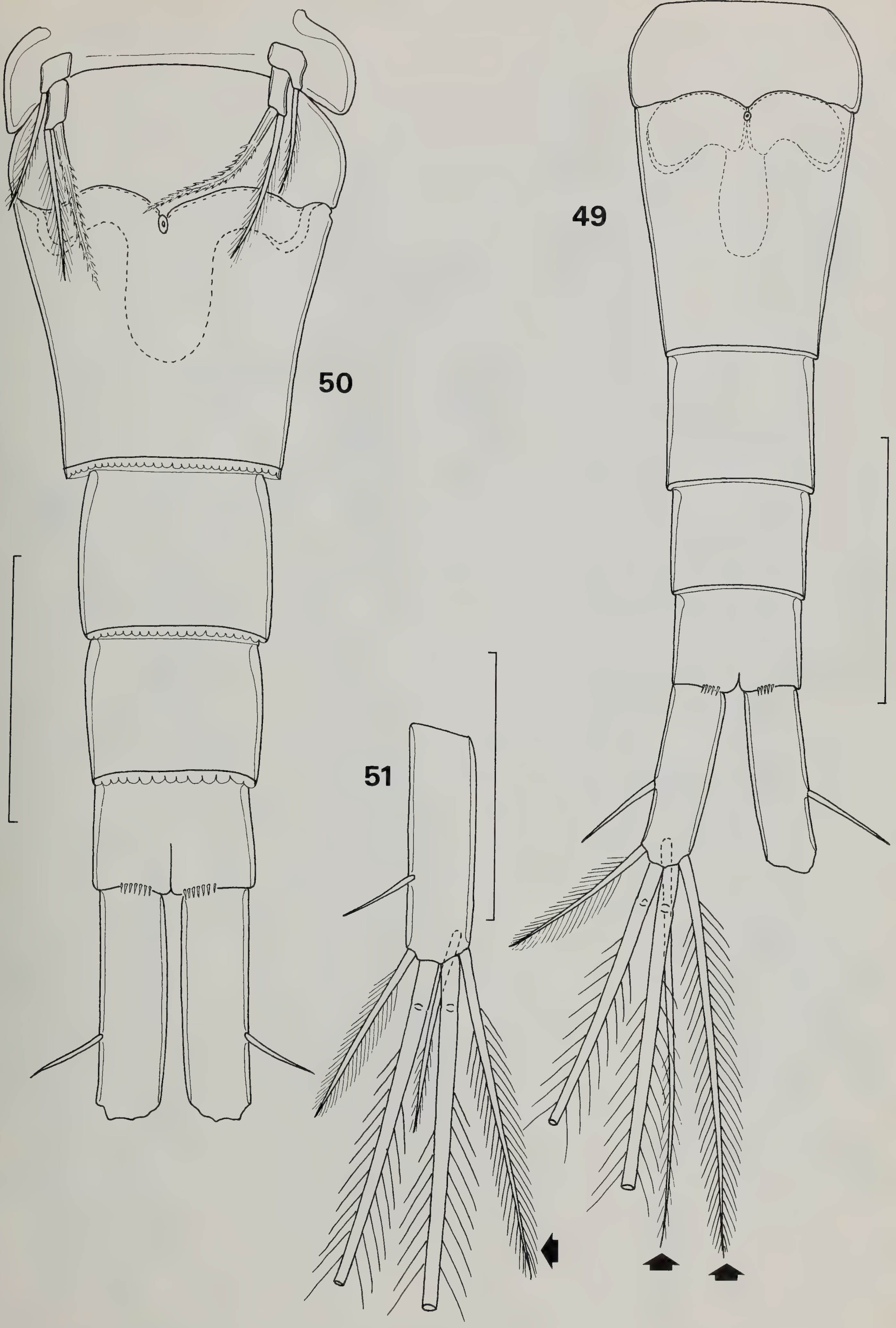
Figs 40–44 *Cryptocyclops bicolor*: 40, anal somite and caudal ramus. *Cryptocyclops linjanticus*: 41, female urosome; 42, leg 4. *Mesocyclops aspericornis*: 43, fifth legs. *Thermocyclops oblongatus*: 44, fifth legs. Scale bars 40, 42–44 = 50µm, 41 = 100µm.



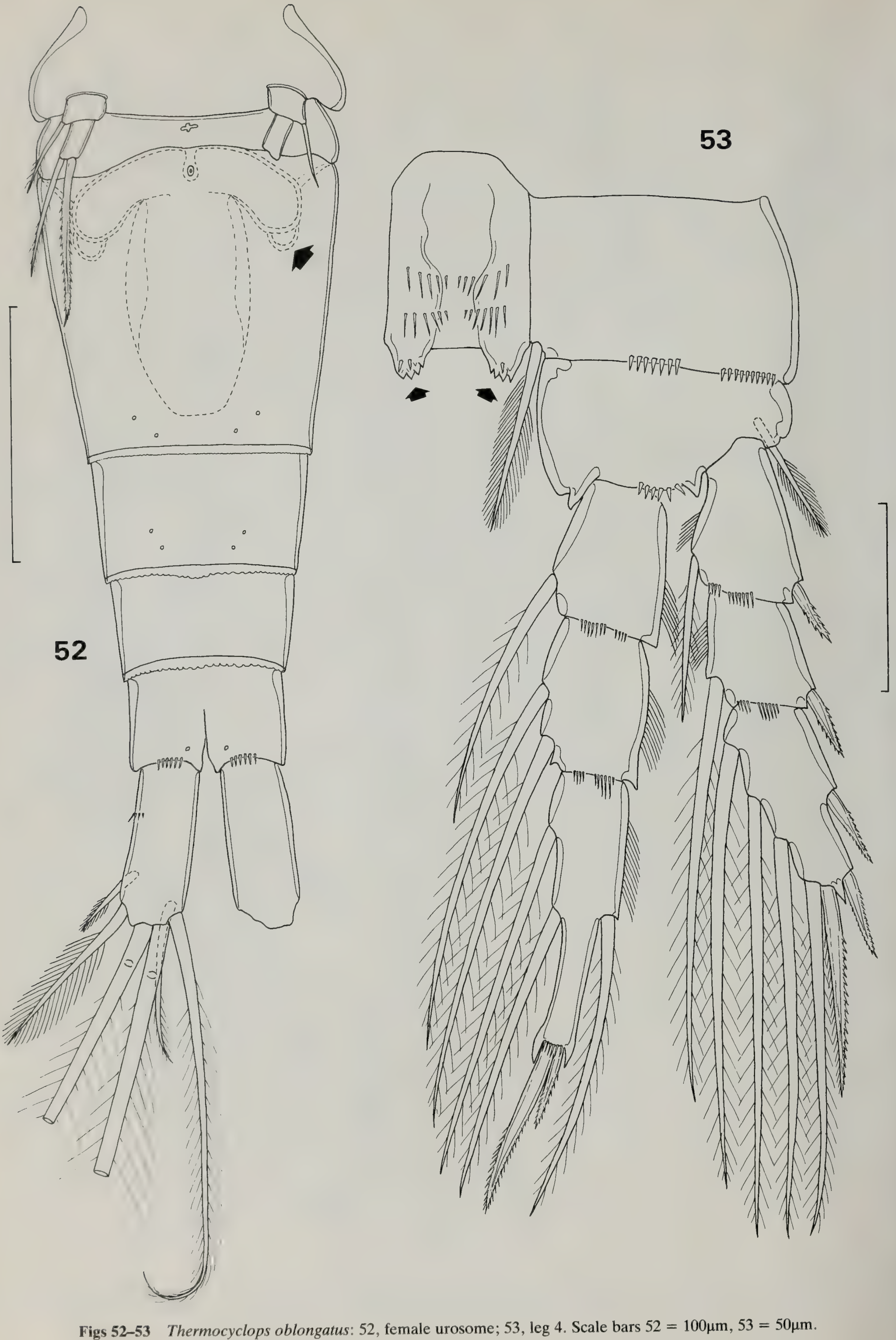
Figs 45–46 *Thermocyclops inopinus*: 45, leg 4. *Thermocyclops neglectus*: 46, leg 4. Scale bars = 50μm.



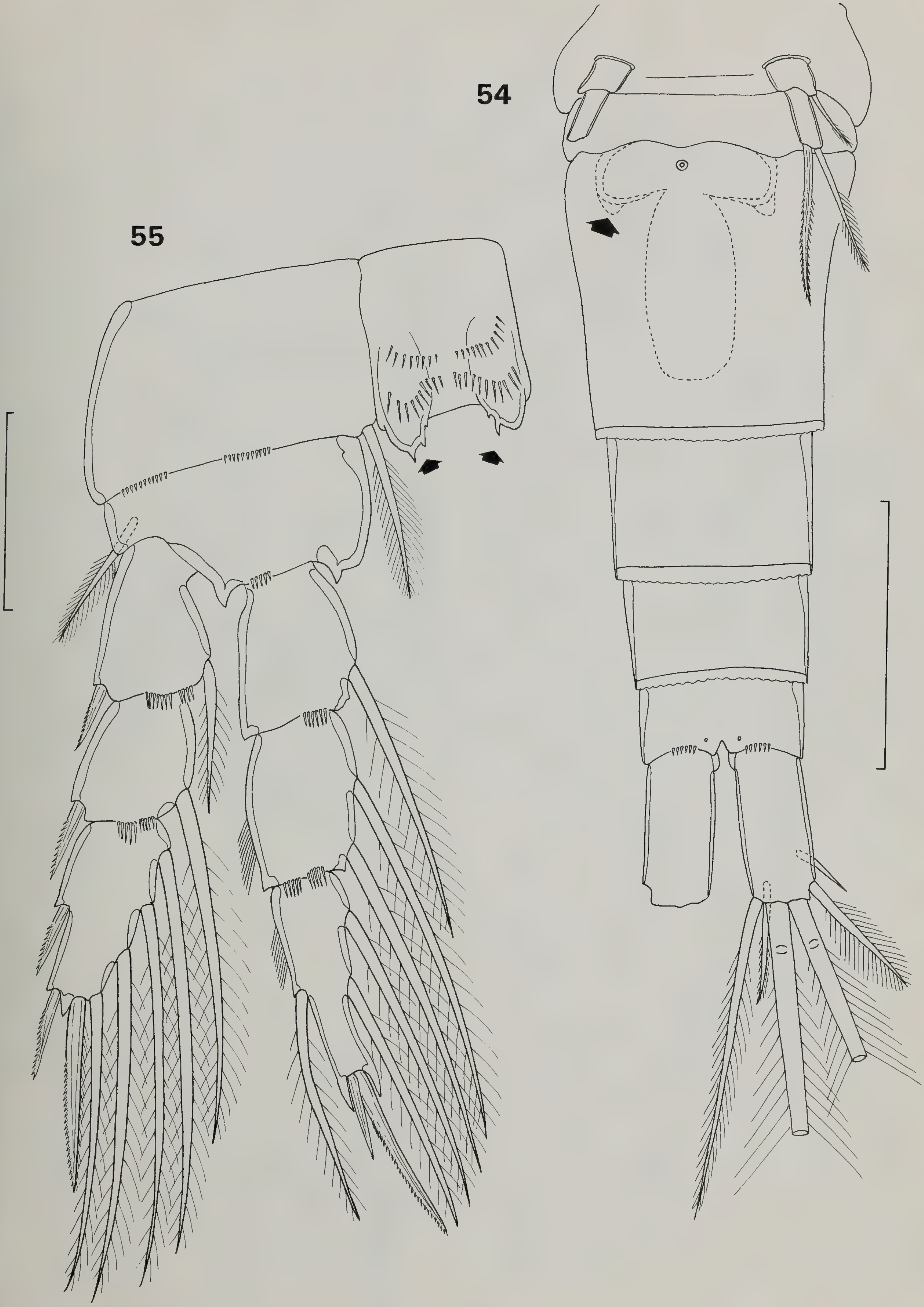
Figs 47–48 *Thermocyclops iwoyensis*: 47, leg 4. *Thermocyclops incisus*: 48, posterior part of urosome and caudal rami, redrawn from Kiefer (1933). Scale bar = 50μm.



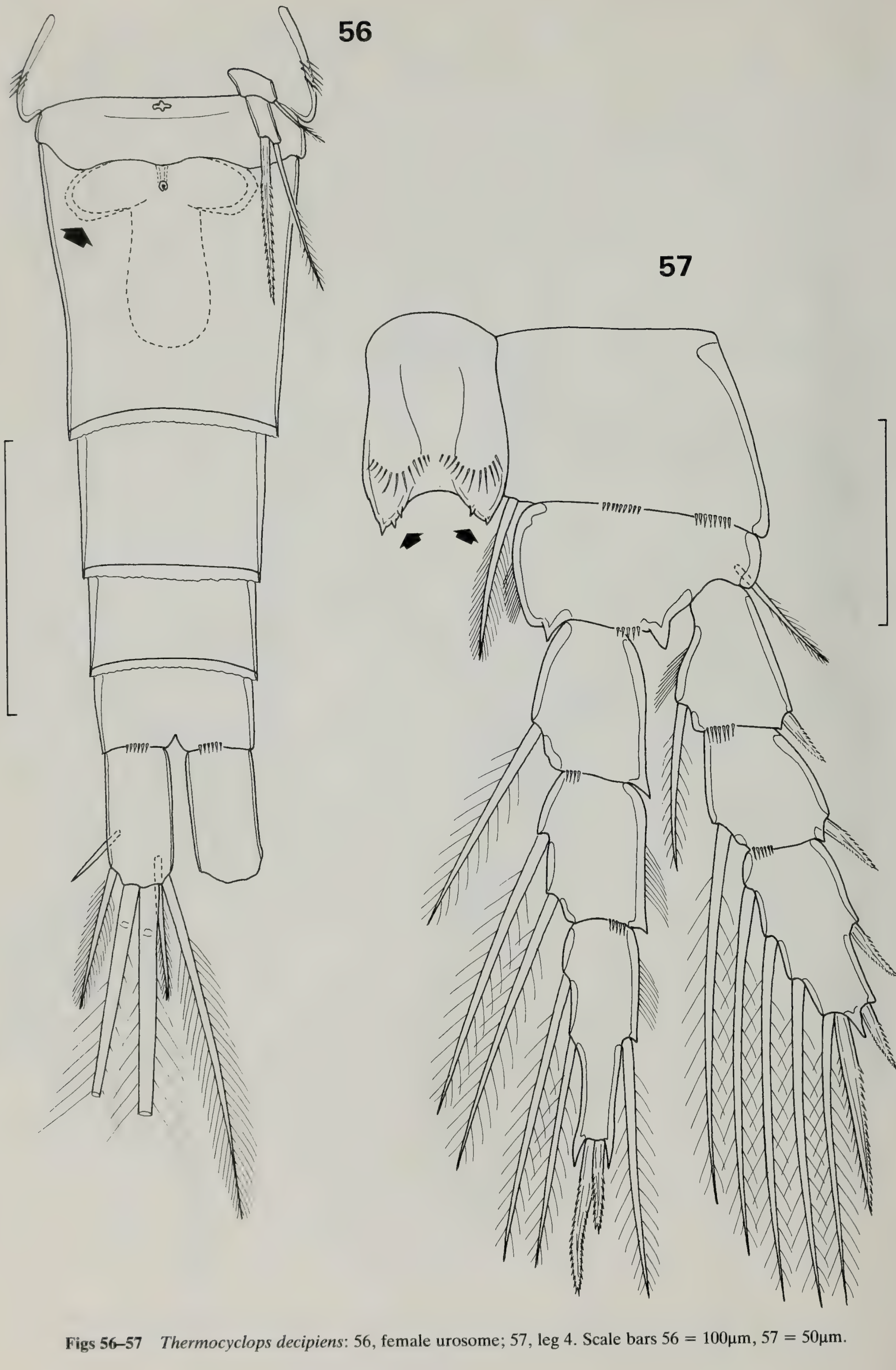
Figs 49–51 *Thermocyclops iwoyensis*: 49, female urosome. *Thermocyclops inopinus*: 50, female urosome; 51, caudal ramus. Scale bars = 100µm.



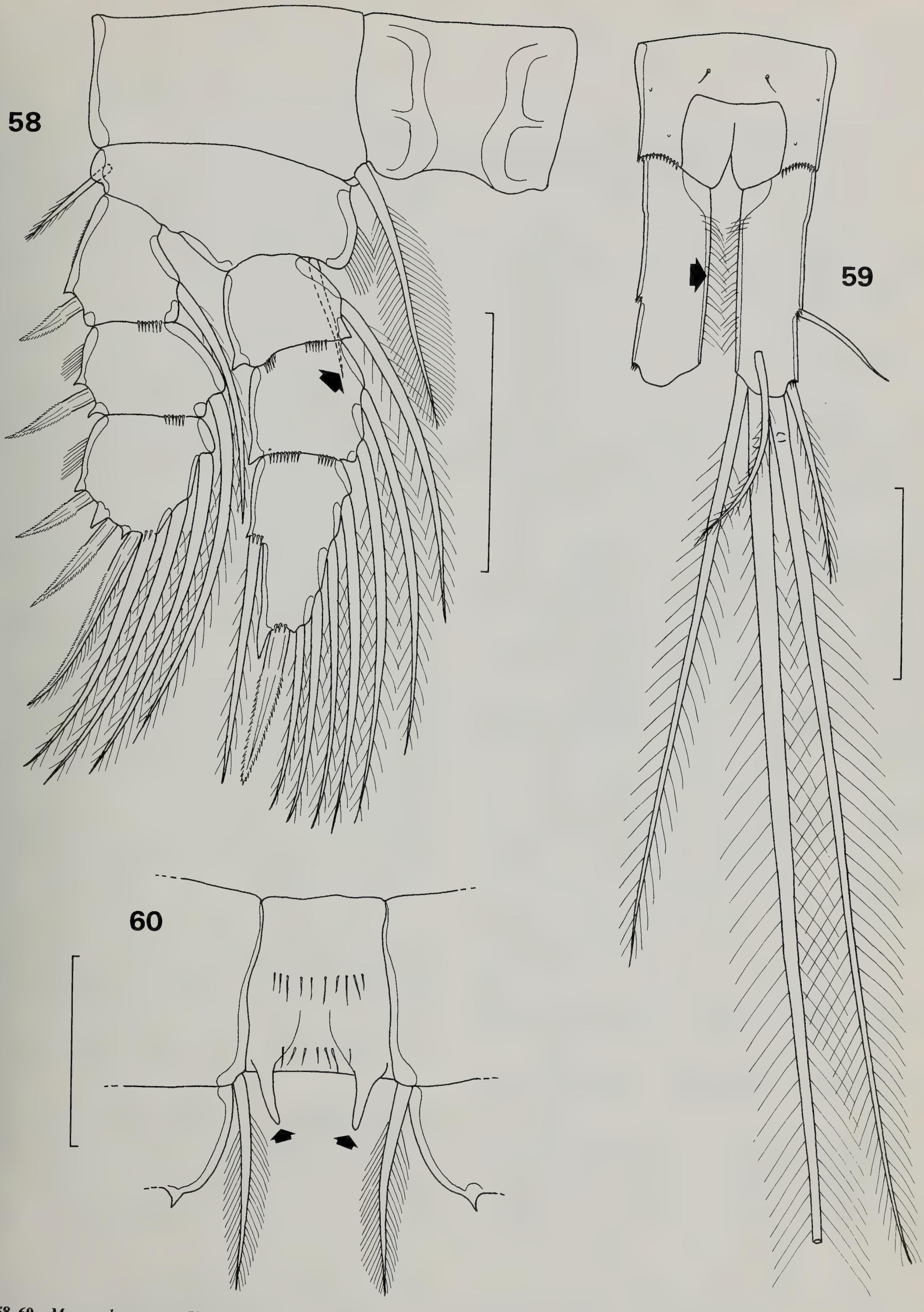
Figs 52–53 *Thermocyclops oblongatus*: 52, female urosome; 53, leg 4. Scale bars 52 = 100µm, 53 = 50µm.



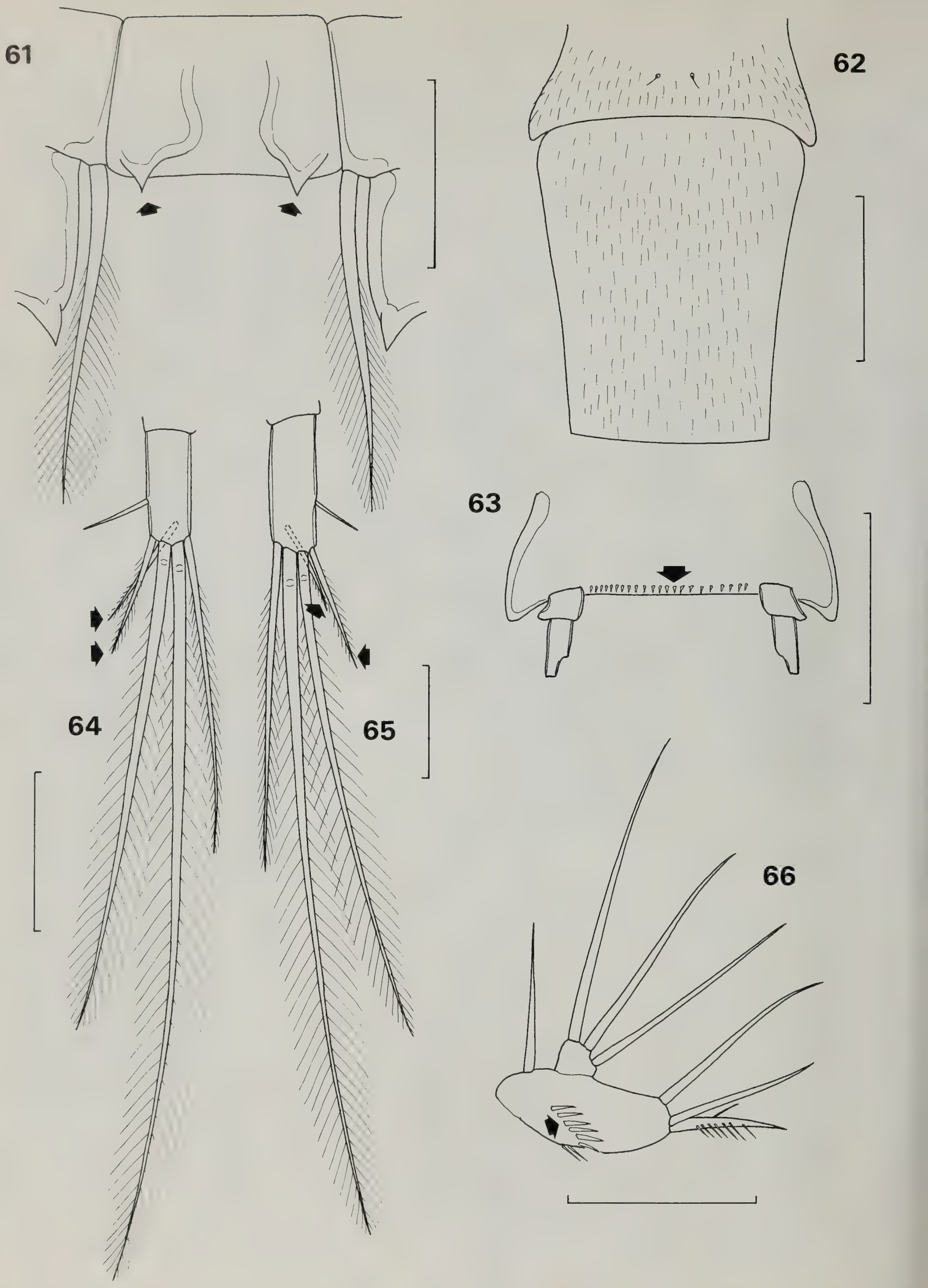
Figs 54–55 *Thermocyclops crassus*: 54, female urosome; 55, leg 4. Scale bars 54 = 100µm, 55 = 50µm.



Figs 56–57 *Thermocyclops decipiens*: 56, female urosome; 57, leg 4. Scale bars 56 = 100µm, 57 = 50µm.



Figs 58–60 *Mesocyclops rarus*: 58, leg 1. *Mesocyclops aspericornis*: 59, anal somite and caudal rami. *Mesocyclops salinus*: 60, syntype female, intercoxal plate of leg 4. Scale bars 58 = 100μm, 59–60 = 50μm.



Figs 61–66 *Mesocyclops aequatorialis similis*: 61, intercoxal plate of leg 4; 65, caudal ramus. *Mesocyclops major*: 62, anterior part of urosome; 63, fifth pedigerous somite, ventral. *Mesocyclops ogunnus*: 64, syntype female, caudal ramus; 66, maxillulary palp redrawn from van de Velde (1984). Scale bars 61 and 66 = 50μm, 62–65 = 100μm.

Mkpani village, Cross River State, Nigeria by Braide, and 3 ♀♀ collected from Obuasi, Ghana by Graham, BM(NH) 1909.12.11.14.23.

28. *Mesocyclops major* Sars, 1927: (Fig. 62–63)

M.major was described from South Africa and was not found again until Van de Velde (1984) revised the African *Mesocyclops* and discovered that *M.major* is widespread South of the Sahara in all climatic belts from hyper-arid to equatorial. It was reported from Nigeria for the first time by Sridhar & Kale (1985) who collected it at Ijere, Oyo State.

MATERIAL EXAMINED. 2♀♀ collected from Mkpani village, Cross River State, Nigeria by Braide.

29. *Mesocyclops salinus* Onabamiro, 1957: (Fig. 60).

This species was described from brackish water at Korodu beach, near the sea at Lagos by Onabamiro (1957). It was not reported after its original description until Van de Velde (1984) recognised it as a widely distributed species in Africa south of the Sahara. Jeje (1988) reported *M.salinus* from several localities south of the river Niger and its major tributary, the river Benue.

MATERIAL EXAMINED. 4 ♀♀ syntypes collected from Korudu Beach, near Lagos, Nigera by Onabamiro, BM(NH) Reg. No. 1957.2.15.1.

30. *Mesocyclops aequatorialis similis* Van de Velde, 1984: (Fig. 61, 65)

There are two subspecies of *M.aequatorialis* found in Africa (Van de Velde, 1984) and although many of the old records of *M.leuckarti* are attributable to this species it is usually not possible to refer to a particular subspecies. *M.aequatorialis aequatorialis* (Kiefer, 1929) is restricted to Lakes Kivu and Tanganyika whereas *M.aequatorialis similis* is widely distributed in Africa south of the Sahara (Van de Velde, 1984). On the basis of known distributions Green's (1962) record of *Mesocyclops leuckarti aequatorialis* is probably referrable to *M.aequatorialis similis*. Jeje (1988) reported *M.aequatorialis similis* present on small numbers in the Nun river at Ikolo, the river Yenagoa and a pool at Yartafki.

MATERIAL EXAMINED. 1♀ collected from South West Nigeria by Onabamiro, BM(NH) Reg. No. 1957.2.15.20. Numerous specimens collected from Mkpani village, Cross River State, Nigeria by Braide.

31. *Mesocyclops ogunnus* Onabamiro, 1957: (Fig. 64, 66)

This species was described from material collected in stagnant pools formed as the river Ogun dried out, at Abeokuta in Nigeria (Onabamiro, 1957). It tolerates brackish and saline waters and is widely distributed in Africa south of the Sahara (Van de Velde, 1984). *M.ogunnus* was reported from various habitats at Ibadan, Benin city, Patani, Aviara, Doro and Nsukka by Jeje (1988).

MATERIAL EXAMINED. 2♀♀ syntypes collected from stagnant pools in the river Ogun at Abeokuta, Nigeria by Onabamiro, BM(NH) Reg. No. 1957.2.15.2.

32. *Mesocyclops rarus* Kiefer, 1981: (Fig. 58)

This species was reported from Nigeria for the first time by Jeje (1988) who found it at a single locality, a pond in Nsukka campus botanical gardens.

MATERIAL EXAMINED. Nigerian specimens of this species were not available; 10 ♀♀, 2♂♂ collected from pond on Muheza Estate, Tanzania by Judith Pell on 20th September 1987, BM(NH) Reg. Nos. 1990.651–660.

33. *Mesocyclops dussarti* Van de Velde, 1984

This species was recorded from Nigeria by Jeje (1988). It occurred in a temporary pool at Port Harcourt, in fish ponds at Moniya, in the river Asaba, and in a lake at Kainji.

MATERIAL EXAMINED. None.

34. *Thermocyclops crassus* (Fischer, 1853): (Figs. 54–55)

This species was first recorded from Nigeria by Lindberg (1950), as *Thermocyclops hyalinus* (Rehberg). It was subsequently re-recorded from South West Nigeria by Onabamiro (1952*a*) under the same name. *T.crassus* was reported from several localities throughout Nigeria by Jeje (1988).

MATERIAL EXAMINED. Numerous specimens collected from South West Nigeria by Onabamiro, BM(NH) Reg. No. 1957.2.15.23, by Egborge from the Oshun River, Nigeria, BM(NH) Reg. No. 1969.10.4.5, and by Braide from Mkpani village, Cross River State, Nigeria.

35. *Thermocyclops neglectus* (Sars, 1909): (Fig. 46)

This species was reported from Okolom by Lindberg (1951) and from South West Nigeria by Onabamiro (1952*a*). Jeje (1988) recorded *T.neglectus* from Opi lake, a temporary pool at Oheorhe, and fish ponds at Moniya.

MATERIAL EXAMINED. 3♀♀ collected from South West Nigeria by Onabamiro, BM(NH) Reg. No. 1957.2.15.22 and 10♀♀ collected by Tetteh from Ghana, BM(NH) Reg. No. 1974.760–770 (as *T.hyalinus*).

36. *Thermocyclops inopinus* (Kiefer, 1926): (Figs. 45, 50–51)

This species was first recorded from Nigeria by Lindberg (1951) who found both sexes at Okolom.

MATERIAL EXAMINED. 1♀ collected from South West Nigeria by Onabamiro, BM(NH) Reg. No. 1957.2.15.25.

37. *Thermocyclops oblongatus nigerianus* Kiefer, 1932: (Figs. 44, 52–53)

This species was described, as *Mesocyclops* (*Thermocyclops*) *nigerianus*, on material collected in Upper Volta (Kiefer, 1932). It is widely distributed throughout Nigeria. It was reported as *Thermocyclops nigerianus*, from South West Nigeria by Onabamiro (1951, 1952*a*, 1952*b*), from Anambra State by Nwosu et al. (1982), from Plateau State by Onwuliri & Obi (pers. comm.), from Kwara State by Abolarin (1979) and Edungbola & Watts (1984), from Ogun State by Ogunba & Kale (1985), and from Oyo State by Edungbola (1984) and Ogunba & Kale (1985).

MATERIAL EXAMINED. Numerous specimens collected by Onabamiro (as *T.nigerianus*) from South West Nigeria, BM(NH) Reg. No. 1957.2.15.21 and from Mkpani village, Cross River State, Nigeria by Braide.

38. *Thermocyclops decipiens* Kiefer, 1929: (Figs. 56–57)

This species was reported from the Sokoto river by Green (1962) and from a reservoir near Ibadan by Imevbore (1965). It was recorded from Oyo State by Sridhar & Kale (1985) as *Thermocyclops neglectus decipiens*. Jeje (1988) found *T.decipiens* to be the commonest Nigerian species of *Thermocyclops* and reported it from a wide range of habitat types and localities.

MATERIAL EXAMINED. 1♀ collected by Onabamiro in South West Nigeria, BM(NH) Reg. No. 1957.2.15.24 and numerous ♀♀ collected from Mkpani village, Cross River State, Nigeria by Braide.

39. *Thermocyclops incisus* Kiefer, 1932: (Fig. 48)

This species was reported from the Sokoto river by Green (1962).

MATERIAL EXAMINED. None.

40. *Thermocyclops iwoyensis* Onabamiro, 1952: (Fig. 47, 49)

This species was described on material collected at Iwoye, South West Nigeria by Onabamiro (1952*a*). It has not been recorded since.

MATERIAL EXAMINED. 2♀♀ paratypes collected on 13 September 1950 by Onabamiro at Iwoye village, Nigeria, BM(NH) Reg. Nos. 1952.11.28.1–2. Numerous additional specimens collected from Mkpani village, Cross River State, Nigeria by Braide.

B. Invalid species

1. *Cyclops brevipes* Brady 1910

This species was treated as incertae sedis by Dussart & Defaye (1985). It was identified as juveniles of *Cyclops* sensu lato by Lindberg (1950).

2. *Diacyclops gauthieri* Green, 1962

This species was established by Green (1962) as *Cyclops* (*Diacyclops*) *gauthieri* and was recorded from the Sokoto river in Nigeria. Green (1962) does not figure the urosome of his material, stating that it was described by Gauthier (1951) from Senegal but was not named. Gauthier's figures (1951: plate XXXI, figures A-D) are clearly of a fifth male copepodid stage of a *Mesocyclops*. The appendages figured by Green (1962) also closely resemble those of a male fifth copepodid of *Mesocyclops*. *Diacyclops gauthieri* is herein regarded as an indeterminate species of *Mesocyclops*, based on male fifth copepodids.

3. *Mesocyclops leuckarti* (Claus, 1857)

The confusion regarding the identification and geographical distribution of *M.leuckarti* has only recently been revealed. Van de Velde (1984) revised the African species of *Mesocyclops* and demonstrated that *M.leuckarti* does not occur in Africa. Similarly, Kiefer (1981) analysed many other records of this species and showed that it extends through Europe into the western part of Northern Asia. All other records of *M.leuckarti* are incorrect. The taxonomic confusion is very significant for studies of the transmission of *Dracunculus* since *M.leuckarti* is by far the commonest name given in the literature as the vector both in Africa and Asia. It has been recorded many times from Nigeria (Brady, 1910, as *Cyclops nigeriae*; Lindberg, 1950, 1951; Onabamiro, 1951, 1952*a*, 1952*b*; Nwosu et al., 1982; Ogunba & Kale, 1985). Without access to the specimens upon which these reports are based it is not possible to reidentify the copepods involved. Some of the *M.leuckarti* records contain sufficent description to allow identification, for example Green (1962), and these are treated in the list of valid species given above.

4. *Eucyclops productus* Kiefer, 1936

This species is known only from Kashmir (Kiefer, 1936; Lindberg, 1939). It was recorded, without description, from Nigeria by Onabamiro (1952*b*). Upon re-examination, Onabamiro's material of *E.productus* (BM(NH) Reg. No. 1957.2.15.10) was found to be indistinguishable from the *Eucyclops serrulatus* collected by him in the same region of Nigeria.

C. Taxonomic remarks

Seven species of *Thermocyclops* are recorded from Nigeria. Some of these species are extremely difficult to identify. The characters used by Jeje (1988) to distinguish between *T.neglectus*, *T.crassus* and *T.decipiens* were found to be unreliable in the present study. *Thermocyclops* is one of the genera that serves as a natural host for *Dracunculus* and the African species of this genus are in urgent need of revision, as Van de Velde (1984) has revised the African species of *Mesocyclops*.

In this study a total of 40 species and subspecies of freshwater cyclopid copepods is recognised from Nigeria. Material of most of these taxa has been examined and figured during the present study. Our primary objective was to provide a well illustrated and easy to use key for Guineaworm researchers. Obvious characters were used in the key whenever possible on the assumption that high resolution compound microscopes would not be readily available to Nigerian field workers. All major characters have been figured and the majority of the figures are original and based upon Nigerian material. Considerable emphasis was placed on the use of Nigerian material in an attempt to avoid identification problems caused by geographical variation. The key is specifically constructed for use with Nigerian material and should be used with caution elsewhere in Africa.

Key to Nigerian freshwater cyclopoid copepods

(adult females only)

1. Female antennule 6–segmented (Fig. 1); distal segment of fifth leg with 4 setae or spines (Figs 2, 5) 2
   Female antennule with 10 or more segments (Fig. 10); distal segment of fifth leg with at most 3 setae or spines (Figs. 7, 9) 3
2. Lateral margins of genital double segment rounded (Fig.

1); inner setae on endopod segment 3 of leg 4 small (Fig. 3) .... ***Halicyclops korodiensis***
Lateral margins of genital double segment with backward-pointing, curved process (Fig. 4); setae on endopod of leg 4 normal (Fig. 6) .... ***Halicyclops pondoensis***

3. Distal segment of fifth leg with 3 setae or spines (Figs. 7, 9, 31) 4
Distal segment of fifth leg with 1 or 2 setae or spines (Figs. 38, 43) 17

4. Fifth leg with 2 free segments, distal segment carrying 2 spines and a seta (Fig. 7) .... ***Macrocyclops albidus***
Fifth leg with at most 1 free segment (Fig. 9) 5

5. Antennule 12–segmented; Fifth leg with 1 spine and 2 setae, arranged 1 apical and 1 marginal (Fig. 31) 7
Antennules 11–segmented; Fifth leg a small plate with 2 setae and 1 spine on flattened distal margin (Figs. 8–9) .... ***Paracyclops affinis***
Antennules 10 or 11–segmented (Fig. 10); Fifth leg incorporated into body segment, with 3 setae or spines on surface (Figs 11–13) 6

6. Inner spine of fifth leg extending just beyond middle of genital double segment; Caudal rami about 2x longer than wide (Fig. 11) .... ***Ectocyclops phaleratus***
Inner spine of fifth leg extending to rear margin of genital double segment, other setae about half length of spine; Caudal rami about 1.4x longer than wide (Fig. 13) .... ***Ectocyclops ilariensis***
Inner spine of fifth leg extending beyond rear margin of genital double segment, other setae almost as long as spine; Caudal rami just over 2x longer than wide (Fig. 12) .... ***Ectocyclops compactus***

7. Seminal receptacle with 2 anterior prolongations (Fig. 21) 8
Seminal receptacle without anterior prolongations (Fig. 27) 11

8. 3 spines on outer and terminal margins of exopod segment 3 of leg 3 (Fig. 14) .... ***Tropocyclops confinis***
4 spines on outer and terminal margins of exopod segment 3 of leg 3 (cf. Fig. 18) 9

9. Inner spine on basis of leg 1 absent (Fig. 15) .... ***Tropocyclops onabamiroi***
Inner spine on basis of leg 1 present (cf. Fig. 58) 10

10. Caudal rami less than 2x longer than wide (Fig. 16) .... ***Tropocyclops mellanbyi***
Caudal rami 2.3 to 3x longer than wide (Fig. 17) .... ***Tropocyclops prasinus***

11. 4 spines on outer and terminal margins of exopod segment 3 of legs 2 and 3 (Fig. 18) 12
3 spines on outer and terminal margins of exopod segment 3 of legs 2 and 3 (Fig. 19) 14

12. Denticle rows present along margins of last 3 antennule segments (Fig. 20) .... ***Eucyclops macruroides***
Strips of smooth membrane present on last 3 antennule segments (Fig. 22) 13

13. Middle seta of fifth leg about 2x longer than inner spine (Fig. 25) .... ***Eucyclops serrulatus***
Middle seta of fifth leg 1.3 to 1.6x longer than inner spine (Fig. 23–4) .... ***Eucyclops agiloides***

14. Antennule short, only 2/3rds as long as cephalothorax; apical segments short and squat (Fig. 26a) .... ***Afrocyclops curticornis***
Antennule reaching beyond rear margin of cephalothorax (Fig. 26b) 15

15. Inner spine on distal margin of endopod segment 3 of leg 4 about twice as long as outer spine (Fig. 28) .... ***Afrocyclops gibsoni***
Inner spine on distal margin of endopod segment 3 of leg 4 longer than, but not twice as long as outer spine (Figs. 30, 32) 16

16. Female body length less than 1.0mm; [ventral spine of male sixth leg reaching rear margin of first abdominal somite] .... ***Afrocyclops ikennus***
Female body length usually more than 1.1mm; [ventral spine of male sixth leg reaching rear margin of second abdominal somite .... ***Afrocyclops doryphorus***

17. Legs 1 to 4 with 3–segmented rami (Fig. 46); fifth leg with 2 distinct segments (Fig. 43) 23
Legs 1 to 4 with 2–segmented rami (Fig. 34); fifth leg comprising 1 distinct segment, with or without a basal segment fused to body somite (Fig. 33) 18

18. Free segment of fifth leg carrying 1 seta and a small spine (Figs. 33, 35) 19
Free segment of fifth leg elongate, carrying a single apical seta, and sometimes fine hairs (Figs. 36, 38) 20

19. Inner apical seta on caudal ramus half length of ramus (Fig. 35) .... ***Metacyclops minutus***
Inner apical seta on caudal ramus about as long as ramus (Fig. 33) .... ***Metacyclops pseudoanceps***

20. Endopod segment 2 of leg 4 with 2 well developed apical spines (Fig. 39) 21
Endopod segment 2 of leg 4 with a very short outer and long inner apical spine (Fig. 42) 22

21. Inner apical seta of caudal ramus 1.8x longer than ramus (Fig. 37) .... ***Microcyclops jenkinae***
Inner apical seta of caudal ramus about as long as ramus (Fig. 36) .... ***Microcyclops varicans***

22. Caudal ramus 4 to 5x longer than wide (Fig. 40) .... ***Cryptocyclops bicolor***
Caudal ramus 3 to 3.5x longer than wide (Fig. 41) .... ***Cryptocyclops linjanticus***

23. Fifth leg with 2 setae inserted distally or subdistally on free segment (Fig. 44) .... **24 (*Thermocyclops* spp.)**
Fifth leg with 2 setae, 1 inserted apically on free segment, the other near middle of inner margin (Fig. 43) .... **30** .... **(*Mesocyclops* spp.)**

24. Projecting lateral fields on intercoxal plate of leg 4 smooth (Figs. 45, 47) 25
Projecting lateral fields on intercoxal plate of leg 4 armed with teeth or spinules (Figs. 46, 53) 27

25. Inner apical seta on caudal ramus less than 2x longer than outer apical seta (Figs. 50–51) .... ***Thermocyclops inopinus***
Inner apical seta on caudal rami more than 2x longer than outer apical seta (Fig. 49) 26

26. Dorsal and inner apical setae on caudal ramus about equal in length (Fig. 49) .... ***Thermocyclops iwoyensis***
Dorsal seta shorter than inner apical seta on caudal ramus (Fig. 48) .... ***Thermocyclops incisus***

27. Lateral wings of seminal receptacles large and recurved posteriorly (Fig. 52) ...... ***Thermocyclops oblongatus***
Lateral wings of seminal receptacles not, or poorly, produced posteriorly (Figs. 54, 56) 28

28. Projecting lateral fields on intercoxal plate of leg 4 forming large toothed process (Fig. 46) .... ***Thermocyclops neglectus***
    Projecting lateral fields on intercoxal plate of leg 4 armed with small spinules (Figs. 55, 57) 29

29. Lateral wings of seminal receptacles with small, posteriorly produced lobes (Fig. 54) ..... ***Thermocyclops crassus***
    Lateral wings of seminal receptacles without posteriorly produced lobes (Fig. 56) .... ***Thermocyclops decipiens***
30 Inner spine on basis of leg 1 present (Fig. 58) .... ***Mesocyclops rarus***
    Inner spine on basis of leg 1 absent 31

31. Inner margin of caudal rami with row of setules (Fig. 59) .... ***Mesocyclops aspericornis***
    Inner margin of caudal ramus devoid of setules 32

32. Intercoxal plate of leg 4 with finger-like processes laterally (Fig. 60) .... ***Mesocyclops salinus***
    Intercoxal plate of leg 4 with lateral processes rounded, or short and pointed (Fig. 61) 33

33. Dorsal surface of genital double segment completely covered with short setules (Fig. 62) 34
    Dorsal surface of genital segment devoid of setules 35

34. Ventral margin of fifth pedigerous somite with row of spinules between fifth legs (Fig. 63); intercoxal plate pf leg 4 with setules on caudal surface.. ***Mesocyclops major***
    No row of spinules on somite between fifth legs; intercoxal plate of leg 4 without setules .... ***Mesocyclops dussarti***

35. Maxillulary palp with row of spinules (Fig. 66); dorsal seta on caudal rami about equal to outer apical seta (Fig. 64) .... ***Mesocyclops ogunnus***
    Maxillulary palp without row of spinules; dorsal seta on caudal rami shorter (about 2/3rds) than outer apical seta (Fig. 65) .... ***Mesocyclops aequatorialis***

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A new species of *Ferdina* (Echinodermata: Asteroidea) from the Sultanate of Oman with discussion of the relationships of the genus within the family Ophidiasteridae.

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Synopsis. A new species of ophidiasterid starfish, from shallow water on the coast of Oman, is described in the formerly monotypic genus *Ferdina*. The diagnosis of the genus given by Clark (1967) is amended to accommodate the new species and a discussion and key are provided to distinguish *Ferdina* from related genera.

INTRODUCTION

The shallow-water Asteroid fauna of Oman and Yemen is not well known and ecological and zoogeographic studies by one of us (Campbell & Morrison (1988) and Campbell, in prep.) have added many species to those listed by Clark & Rowe (1971) and Price (1982).

The south coast of Oman, although lying between the latitudes of 19°00′N and 16°40′N has marked variation in temperature and nutrient levels due to seasonal upwelling along the very narrow continental shelf, particularly in the vicinity of Sadh. The coast is affected by the South-West Monsoon for four months of the year (June to September); this brings marked changes in the sea water conditions with temperatures falling from 28°C (pre-monsoon) to 18°C (monsoon) and nutrients rising from 0.4–0.6 micrograms dm^{-3} (pre monsoon surface phosphate) to > 1.0 micrograms dm^{-3} (post monsoon). Surface nitrate over the same period rises from <0.5 micrograms dm^{-3} to >10.00 dm^{-3}. The fall in water temperature and the sudden influx of nutrients results in a rapid growth of macroalgae. Campbell & Morrison (1988) give a fuller account of the physical and biological features of the region.

These conditions result in a mixed fauna of tropical and temperate species. The asteroid fauna, however, consists entirely of tropical species or endemic species with tropical affinities.

One of the latter is a new species described herein.

FERDINA Gray

Ferdina Gray, 1840: 282; 1866: 12–13; Perrier, 1875: 183; Fisher, 1919: 370; H. L. Clark, 1921: 58; Livingstone, 1931: 305, A. M. Clark, 1967: 191–193.

Type species. *Ferdina flavescens* Gray, 1840; designated by Fisher, 1919.

Diagnosis. After Clark (1967), amended.

A genus of Ophidiasteridae with the abactinal skeleton consisting of irregularly placed larger plates superimposed on close fitting smaller ones leaving space between for small papular areas with one to five pores in each; an indistinct carinal series of plates may be evident; the limits of the underlying plates are concealed by continuous granulation (granules even sized or markedly larger on the convex plates than between them); superomarginal plates meet inferomarginals at the base and tip of the rays, elsewhere the superomarginals may be separated from the inferomarginals by intermarginal plates which lie between the irregular, or alternating large and small superomarginals and the regular series of inferomarginals; actinal and adambulacral plates concealed by continuous granulation, extending partway up the outer side of the furrow spines: adambulacral plates with a single row of short blunt furrow spines; actinal papulae restricted to occasional ones at the lower corner of the inferomarginal plates.

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Species included: *Ferdina flavescens* Gray, 1840; *Ferdina sadhensis* sp. nov.

Discussion. The genus *Ferdina* was erected for the species *F. flavescens* and *F. cumingii* Gray, 1840. The two species were more fully described by Perrier (1875) and the description of *F. flavescens* was expanded by de Loriol (1885). Livingstone (1931) restricted the genus *Ferdina* to *F. flavescens* and a new species, *F. heffernani* assigning *F. cumingii* to a new genus, *Neoferdina*, characterised by having some marginal plates bare of granules. A. M. Clark (1967) recognising that *F. heffernani* was unlike *Ferdina* in many respects, re-defined *Ferdina* and erected a new genus *Celerina* of which *F. heffernani* became the type species. Jangoux (1973) re-defined *Neoferdina* including several points omitted by Livingstone, but omitting the important point that the superomarginals are usually more conspicuous than in *Ferdina*. James (1973) described the genus *Paraferdina* for the new species *P. laccadivensis* which differs from *Ferdina* in having fairly large, regular superomarginal plates, and from *Neoferdina* in having all plates completely covered by granules. *P. laccadivensis* is redescribed and a second species of *Paraferdina* described by Marsh & Price (1991). Liao (1982) described the genus *Sinoferdina*, with type species *S. gigantea* from China. This genus differs from *Ferdina* and *Paraferdina* in having some bare marginal plates and from *Neoferdina* in having small, fairly regularly arranged abactinal plates with a distinct carinal series, none of which is bare, and in having smaller less conspicuous superomarginals. *Ferdina* was then left as a monotypic genus to which a second species is now added.

The genera *Ferdina, Neoferdina, Paraferdina* and *Sinoferdina* are here regarded as forming a natural group based principally on the character of the actinal surface and furrow armature. They are distinguished from all other ophidiasterids by having the adambulacral armature in a single series of blunt-ended furrow spines with at least half their length concealed, on the outer side, by a thick, granule-covered integument. The actinal surface is covered by small granules with little, if any, difference in size between those on the plates and between them, however, the latter are usually conspicuous because of their contrasting colour.

Celerina, a monotypic genus separated from *Ferdina* by A. M. Clark (1967), also has a single series of adambulacral spines but these are generally sharply pointed and not at all covered by granulated skin. In *Celerina* the spines on the oral plates, except those at the apex of the jaw, are smaller than the furrow spines, while in the *Ferdina* group they are indistinguishable from the furrow spines. *Celerina* resembles *Fromia monilis* in colour pattern, and arrangement of abactinal and marginal plates and is here regarded as having its closest affinity with *Fromia* despite its lack of actinal papulae and differences in furrow armature.

Ferdina, Neoferdina, Paraferdina and *Sinoferdina* have broad-based tapering arms with usually little regularity in abactinal plate arrangement; the papulae are single or in small groups and are usually confined to the abactinal surface but in *F. sadhensis* they also occur intermarginally and sometimes between the inferomarginal plates.

As noted by Clark (1967) *Ferdina* seems to occupy an isolated position within the family Ophidiasteridae and this statement applies equally well to the other three genera of the *Ferdina* group. However, despite their very different furrow armature, the nature of the abactinal skeleton, with larger abactinal plates superimposed on a reticulum of smaller plates in the two *Ferdina* species is similar to some species of *Nardoa* and *Gomophia* and a relationship may be inferred.

Key to the *Ferdina* group of genera.

1	Abactinal, marginal and actinal plates with a continuous covering of granules	2
1^1	Some marginal plates bare centrally	3
2	Abactinal plates irregular in size with larger convex plates superimposed on close fitting smaller ones, no regular longitudinal or transverse series of plates; supero marginals not in a regular series except at base and tip of arms, not easily distinguished from abactinal plates	***Ferdina***
2^1	Abactinal plates irregular in size but longitudinal and transverse series often evident; superomarginals in a regular series, conspicuous	***Paraferdina***
3	Abactinal plates irregular in size and arrangement but transverse and longitudinal rows are sometimes evident; superomarginals conspicuous when viewed from above; usually some abactinal plates as well as marginals bare centrally	***Neoferdina***
3^1	Abactinal plates small, numerous, fairly regularly arranged, with a distinct carinal series; superomarginals not conspicuous when viewed from above; no bare abactinal plates	***Sinoferdina***

Ferdina sadhensis sp. nov. Figs 1–3

Holotype. BMNH 1990. 4.4.1 (dry)

Type locality. Sadh, near Wadi Haart, Sultanate of Oman, 17°04′N, 55°06′E, 6 m.

Coll. L. Barratt, 7 Oct. 1983 (831007, 2K7)

Material. In addition to the holotype, three paratypes (dry) and one other specimen (dry). Paratype 1, WAM 427–90, Hoones Bay east of Marbat, Dhofar, Sultanate of Oman, 5 m., coll. M. Morrison, 8 April 1988; paratype 2, USNM E41400, Urchin Pt., 16 km east of Marbat, Dhofar, Oman, 8–10 m., coll. M. Morrison, 5 Jan. 1990; paratype 3, University of Singapore, ZRC. 1990. 11806, same collection data as paratype 2; one specimen, A. C. Campbell collection, cat. no. 206030204, Urchin Pt., Oman, 13 m, rock, coll. M. Morrison, 5 April 1990.

Etymology. The species name honours the villagers of Sadh, Sultanate of Oman, who contributed much to the work of one of us (A. C. C.).

Description of holotype. (Figs 1a-c, 2, 3a-c, g) The specimen has a small disc with five rays, constricted at the base then inflated to about 1/3 R from where they taper to a fairly acute tip. R = 53.8 to 56.2 mm (mean = 55.0 mm), r = 13.4 to 14.2 mm (mean = 13.8 mm), R/r = 3.99/1, br at base of arms is 15.8 mm, at the widest point is 17.0 mm and 10 mm from the arm tip it is 8.3 mm.

The abactinal skeleton consists of a mixture of large and small convex plates (fig. 3a). When the skeleton is cleaned some of the large plates are seen to lie on top of the small plates which form a close meshwork as described by A. M. Clark (1967) for *Ferdina flavescens*. There is little order in the arrangement of the plates but an indistinct carinal series of

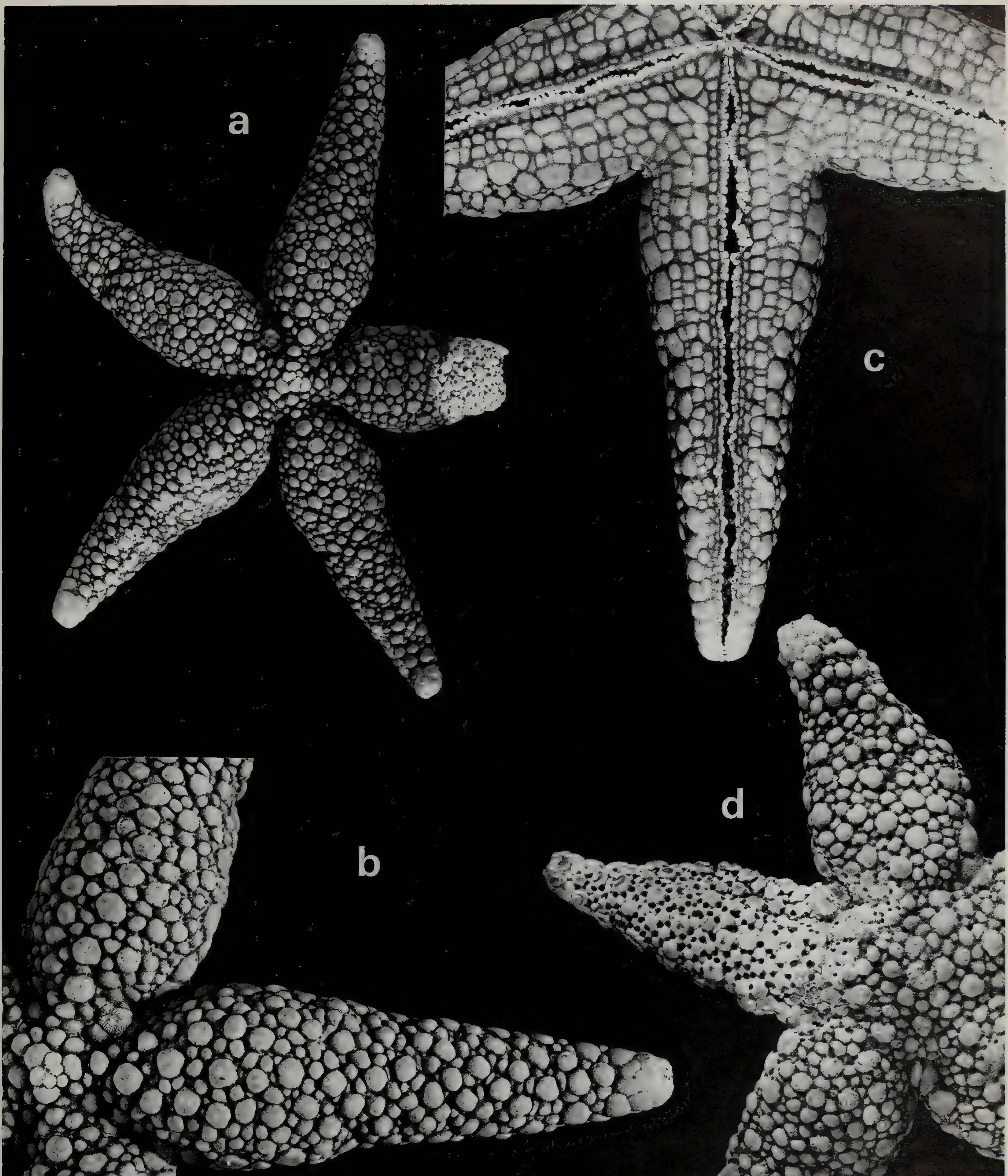

Fig. 1 *Ferdina sadhensis* n. sp., a, b, abactinal views of holotype (BMNH 1990.4.4.1, R/r = 55/13.8 mm); c, actinal view of holotype; d, abactinal view of paratype 1, arm on left denuded (WAM 427.90, R/r = 51.15/15.4 mm).

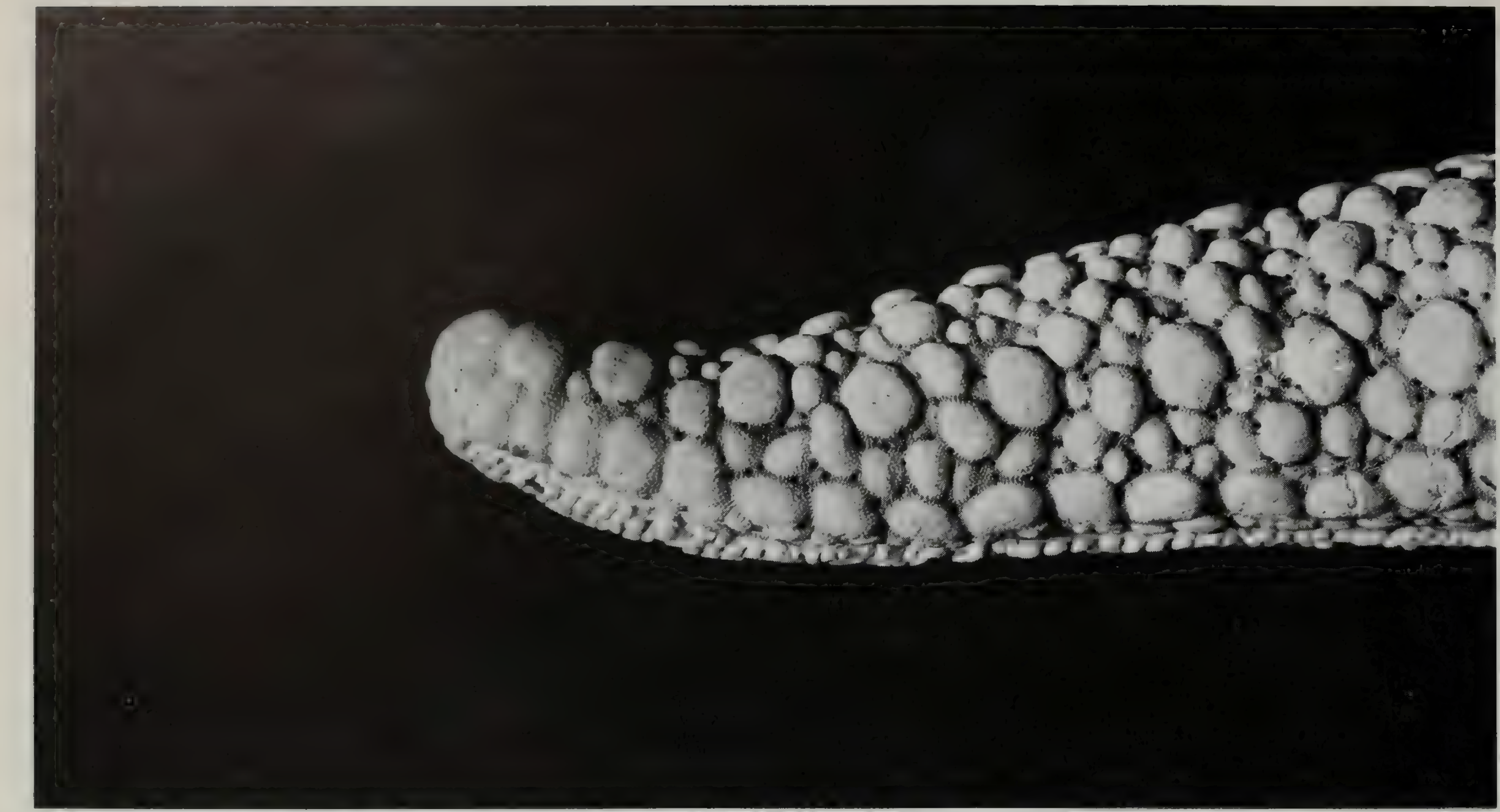

Fig. 2 *F. sadhensis* n. sp., lateral view of arm of holotype to show superomarginal, intermarginal and inferomarginal plates.

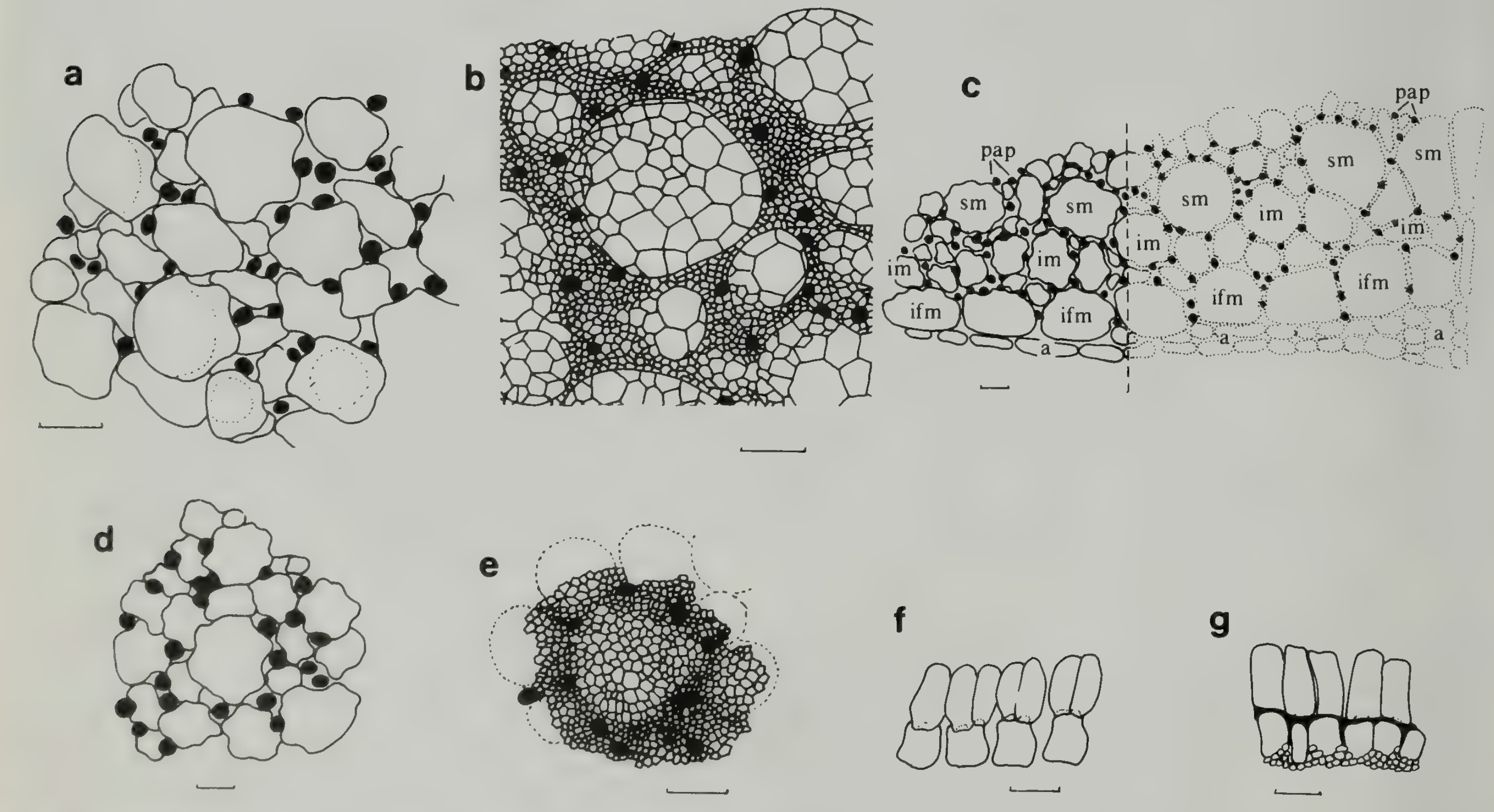

Fig. 3 *F. sadhensis* n. sp., a, abactinal plates of proximal part of arm, denuded (holotype); b, granulation of abactinal arm plates (holotype); c, lateral view of proximal half of arm, partly denuded (to left of dashed line), showing superomarginals (sm), intermarginals (im), inferomarginals (ifm) and some of the actinal plates (a), first marginals on right (holotype); d, abactinal plates of proximal part of arm, denuded (paratype 1); e, granulation of an abactinal arm plate (paratype 1); f, adambulacral plates and furrow spines, viewed from the furrow (paratype 1); g, oblique view across ambulacral furrow (black) showing outer, granule covered face of near side spines and inner surface of far side furrow spines (holotype). Papular pores (pap) shown black (figs a-e). (Scale bar = 1 mm.)

large plates (to 3.0 mm diam.) alternating with one or more smaller plates (*c.* 1.0 mm diam.) can be distinguished. Either side of the carinal series, and separated from it by an irregular series of smaller plates, is an indistinct row of large dorsolateral plates, alternating irregularly with small plates. The remainder of the abactinal plates of the disc and arms are of mixed sizes mostly smaller than the carinal series; both large and small plates are notched for papulae (6–8 notches around the larger plates).

At the base of the ray there are 11 plates across the arm between the first superomarginals and 10 mm from the arm tip there are five plates (two large and three small) across the ray.

The madreporite is roughly four sided, situated nearer the margin than the centre of the disc. It measures 3.4 × 3.2 mm and is fairly irregularly and coarsely grooved. The anus is surrounded by about 15 wedge shaped to polygonal granules, crowded by five convex plates, then three larger convex plates.

The superomarginal plates match the inferomarginals in the arm angle where the first one or two pairs are adjacent (fig. 3c). Beyond this the inferomarginals continue as squarish plates (*c.* 3 × 3 mm), gradually decreasing in size towards the arm end (fig. 2); the inferomarginals number 23. The superomarginals diverge from the inferomarginals and are separated from them by intermarginal plates after the first two plates in the arm angle (figs 2, 3c). The superomarginal plates alternate irregularly with one or two small plates until near the arm end where they again lie in contact with the inferomarginals. On some rays the superomarginal series becomes so irregular that it is hard to distinguish. The larger superomarginals vary in shape, oval to polygonal, *c.* 3.5 × 3.0 mm, decreasing slightly in size distally; they number 25 including the small plates. The two marginal series are separated by 1–2 irregular series of small intermarginal plates (numbering up to 25), from the second superomarginal to the penultimate.

The terminal plate is bare apart from a few large granules and measures 1.4 to 1.8 mm in diameter.

The actinal plates are in 4 rows in the arm angle (fig. 1c). The row next to the adambulacrals extends to the 16–18th inferomarginal, the second row to the 15th (14–16th) inferomarginal, the third row to the 6 or 7th inferomarginal and the 4th row to the second or third inferomarginal. The innermost row of actinal plates starts from a single large square plate abutting the oral plates in three arm angles, in the other two this is unequally divided into two.

The adambulacral plates are smaller than the adjacent actinal plates. The furrow spines are equal or subequal, peg-like, truncate, flattened oval in section, usually two per plate (fig. 3g); the oral spines number 3–4 on each oral plate and are indistinguishable from the furrow series. The adambulacral armature is in a single series with no subambulacral spines.

The large, convex abactinal plates are covered by close-fitting, flat-topped polygonal granules from 1.1 mm diameter to 5/linear mm; on the smaller convex plates the granules are flat-topped or slightly convex, 1.5 to 6/linear mm. Between the plates the granules are very small, 8–9/linear mm (fig. 3b). The superomarginals and inferomarginals are fairly evenly granule covered with 5–6/mm, occasionally with a few larger granules. The actinal plates are covered by fairly even sized polygonal granules (6–7/mm) with smaller granules between the plates (8–9/mm). The actinal granulation extends partway up the outer side of the furrow spines.

There are no crystal bodies on any of the plates. Papulae occur singly or in small groups of 3–5 abactinally; they also occur intermarginally and between some of the inferomarginal plates and at the lower corners of some inferomarginals but there are no pores among the actinal plates.

Colour (dry). Granules on the raised plates are buff, between the plates deep claret red; actinally, granules on the plates are buff with those between the plates deep magenta.

PARATYPE 1. WAM 427–90, (figs 1d, 3d-f) has R of 50.8 to 51.5 mm (mean 51.15), r = 15.4 mm, R/r = 3.3/1; br at arm base = 17.0 mm, at its widest point 18.5 mm and 10 mm from the arm tip it is 9.6 mm.

The general appearance is very similar to that of the holotype, with the largest abactinal plates measuring 3.0 mm diameter (fig. 3d). However the granules on the large plates are more uniform in size and much smaller, 3–5/linear mm (fig. 3e). There are 23 superomarginal plates and 24 inferomarginals. The actinal plates are in three rows with only 1 or 2 plates of a 4th row. The innermost row extends to 13–16th inferomarginal, the second row to the 10–12th and the third row to the 3–5th inferomarginal.

The furrow spines are as described above except that in the paratype the tips are rounded, not truncated (fig. 3f). There are 3–4 oral spines. Papulae occur singly and there are none between or below the inferomarginals.

PARATYPE 2. USNM E41400, has R of 46 to 50 mm (mean 48), plus two shorter regenerating arms, r = 12 mm, R/r = 4.0/1; br at arm base = 12.5 mm, at its widest point 13 mm and 10 mm from the arm tip it is 7.5 mm.

The general appearance is very similar to that of the holotype and paratype 1 except that the arms are more slender and hardly constricted at the base.

There are eight abactinal plates across the arm base between the superomarginals and five across the arm 10 mm from the tip. The madreporite is triangular, flanked by three rectangular to semicircular convex plates with their longest sides abutting the madreporite. The superomarginal plates are very irregular in size, shape and position except for a prominent first pair and 3–4 regular plates near the arm end; intermarginal plates are found in some arm angles, in others they start after the first or second superomarginal, on some arms they extend to about three quarters of the arm length. The actinal plates are in 3–4 rows at the arm base.

The large convex abactinal plates are covered by close packed, polygonal, slightly convex granules of mixed sizes, 2–6/mm with small interstitial granules numbering 8–9/mm; the actinal plates have 5–6 granules/mm with interstitial granules numbering 7–8/mm. Papulae occur singly with about eight around large abactinal plates, two intermarginal series and none below the inferomarginals.

The colour is as described for the holotype but slightly faded.

PARATYPE 3. University of Singapore, ZRC. 1990. 11806, has R of 47 to 56 mm (mean 53.6), plus one regenerating arm, r = 11.5 mm, R/r = 4.6/1; br at arm base = 14 mm, widening to 16–17 mm at one third R then tapering to br of 7.5 mm at 10 mm from the arm end. One arm, regenerating from the base, originates under the disc and has parallel sides with br of 8.3 mm.

There are eight abactinal plates across the arm base, reducing to five at 10 mm from the arm end. The madreporite is triangular, flanked by five plates. The superomarginal plates are very irregular except at the base and end of the arms; intermarginal plates commence after the first or second superomarginal.

The large convex abactinal plates have close packed, polygonal granules, 3–6/mm, the actinal plates have 6 granules/mm with interstitial granules numbering 8/mm. Papulae occur singly or in pairs abactinally and intermarginally with a few between the inferomarginals, none below.

The remaining specimen (Campbell collection) has R/r of 48/11.5 mm = 4.2/1, br = 12.5 mm at base and 7.0 mm at 10 mm from arm tip, the arms are not inflated at one third R or constricted at base.

This specimen has more regular superomarginal plates on some arms where in places large and small plates alternate; intermarginal plates are fewer than in the other specimens. The granulation approaches that of the holotype with granules of very mixed sizes, 1 to 5/mm on some convex plates, the interstitial granules are very small, 9/mm; on the actinal plates there are 5–6 granules/mm with interstitial granules 9/mm.

The colour is as described for the holotype except that the arm tips are cream and the interstitial granules on a regenerating arm are dark brown.

Variation. The holotype is the largest specimen with R/r of 55.0/13.8 mm (3.99/1), the smallest has R/r of 48/11.5 mm (4.2/1), R/r varies from 3.3/1 to 4.6/1; br at the arm base varies from 12.5 to 17 mm, at the widest point from 13 to 18.5 mm and 10 mm from the arm end from 7.0 to 9.6 mm.

All the specimens have a mixture of large and small convex abactinal plates with flat to slightly convex polygonal granules of very mixed sizes. The largest granules are 1.1 mm in diameter on the holotype but another specimen has granules 1 mm in diameter, they range from <1 to 6/mm with interstitial granules fairly uniform at 8–9/mm.

Superomarginal plates are generally very irregular except at the arm base and end but one specimen has a distinct superomarginal series on some arms with a tendency for large and small plates to alternate. This specimen has few intermarginal plates but they are well developed in the others.

The colour pattern is very uniform and more or less retained in the dry specimens which were compared with an underwater colour photograph taken at Urchin Point at 18 m depth. This shows yellowish buff convex plates with wine red interstitial granules except on a regenerating arm where they are dark brown, the arm tips are cream.

Habitat. Sublittoral, collected between 5 and 13 m and photographed at 18 m. It appears to live on metamorphic rock encrusted with red coralline algae and supporting brown turf algae. Hard corals, principally *Acropora* spp., occur at all the sites but there is no evidence that *F. sadhensis* is coral associated. Forests of the brown alga *Sargassopsis* sp. develop thick growths, between one and two metres tall, in the zone populated by *F. sadhensis* following the South-West Monsoon.

Distribution. At present known only from the south coast of Oman.

Remarks. On first examination the present specimens were thought to represent a new genus but the difference from *Ferdina*, as diagnosed by Clark (1967), were found to be insufficient to justify excluding them from the genus *Ferdina*. *F. sadhensis* is thus the second species of the genus *Ferdina*. Rather than erect a new genus the generic diagnosis (Clark 1967) is modified slightly to take account of the new species.

F. sadhensis differs from *F. flavescens* in having swollen rays sometimes constricted at the base and tapering to a narrow tip; more convex abactinal plates; a greater difference between the size of granules on the abactinal plates and those between them and, in the holotype at least, distinct superomarginals with intermarginals between supero- and inferomarginals.

Perrier (1875), de Loriol (1885) and Clark (1967) note that the skeletal plates of *F. flavescens* are concealed by a uniform coat of fine granules, however in Livingstone's enlarged figure of the holotype (1931, pl. 22, fig. 3) there is a noticeable difference in the size of granules on the convex plates compared to those between them, but less so than in *F. sadhensis*.

The actinal surface of the new species closely resembles that of *F. flavescens* and *Neoferdina* spp in having the granule covered skin extending part way up the outer side of the single row of furrow spines. As in *Neoferdina* the actinal plates are outlined in a contrasting colour.

The genus *Ferdina* is apparently confined to the Indian Ocean, west of 60°E, between 20°N and 20°S, however *N. flavescens* has only been found in Mauritius and *F. sadhensis* only in Oman.

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The morphology and phylogeny of the Cerastinae (Pulmonata: Pupilloidea)

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Synopsis. A cladistic analysis of cerastine genera has shown that they represent a monphyletic unit clearly distinct from the selected outgroup, the northern Enidae *sensu stricto*. The Cerastinae are broadly separable into two major clades, the more advanced, or at least more highly differentiated of which is characterised by a pseudosigmurethrous excretory system, as well as certain modifications to the reproductive system. A number of these character-state changes may be interpreted as reflecting a progressive trend towards a more xerophilic lifestyle in both clades, but which is more pronounced in pseudosigmurethrous genera. This has led to a high degree of homoplasy in certain characters. A new character, the caudal crest, is described for the first time and, within the orthurethra, appears to be restricted to the more primitive genera of Cerastinae.

INTRODUCTION

The cerastines were first recognised as being taxonomically distinct from northern representatives of the orthurethran land-snail family Enidae (Buliminidae) by Hugh Watson (1920) who, in a discussion of relationships within the Pupilloidea, commented 'there can be little doubt that *Pachnodus* and its allies should be placed in a separate subfamily from the Palaearctic forms, or perhaps even a distinct family'. The name Cerastinae was formalized by Wenz (1923) in his treatment of Miocene fossil *Cerastus*. Two years later Steenberg (1925), having discussed further the anatomical differences between northern and southern forms, proposed the family name Pachnodinae for the latter. Like Watson, Steenberg was equivocal as to whether the group should constitute a family or subfamily, reflecting the problems which then existed, and indeed still exist, in understanding the family-group taxonomy of the Pupilloidea.

The current concept of the Cerastinae is as a subfamily within the Enidae *sensu lato* (*eg*. Zilch, 1959; Tillier, 1989). However, Mordan (1984; 1986) has reviewed the anatomy of the two groups and argued that the differences between the northern enids and the cerastines are probably of sufficient magnitude for the latter to warrant full family status within the Pupilloidea, although formalisation of this was deferred pending a better knowledge of related orthurethran families. Furthermore, he pointed out that it was difficult to find synapomorphic characters to unite the Cerastinae and the northern Enidae as sister groups in a cladistic sense. Most recently Nordsieck (1986) has given the group family status as the Cerastuidae, which, together with the Buliminidae, form the superfamily Buliminoidea according to his classification.

The cerastines are of considerable interest from a biogeographical viewpoint, having a highly disjunct southern distribution centred on the Afro-tropical region, but extending to India and Australia, and there has been some uncertainty as to whether this represents an ancient vicariant pattern or is simply the result of more recent dispersal events (Mordan, 1984; Nordsieck, 1986). The importance of clearly defined phylogenetic hypotheses as a prerequisite to biogeographic interpretation has frequently been stressed (*eg*. Wiley, 1981; Humphries & Parenti, 1986). The present paper assesses the phylogenetic relationships between the genera and subgenera of Cerastinae using cladistic analysis; a second paper (Mordan, in press) considers the biogeographic implications of the resulting cladogram.

INCLUDED TAXA

In the most recent comprehensive treatment of the Cerastinae, Zilch (1959) listed a total of fifteen genera and subgenera to which a further two, *Amimopina* Solem, 1964 and *Altenaia* Zilch, 1972, have since been added. There is now at least partial published data on the soft anatomy of eleven of these taxa (see Table 1), and this has now been supplemented by further dissections of all of these except *Altenaia* (see Appendix for details of the dissections). As the cladistic analysis is based largely on characters of the soft anatomy, only taxa in the table are included; *Altenaia* is omitted from the analysis, however, as the specimen of *Altenaia connivens* (L. Pfeiffer) referred to in Zilch's paper cannot be traced (R. Janssen, in litt.) and there is therefore insufficient information on the genus. Following Connolly (1939), two forms

Table 1 Principal published sources of anatomical information on the Cerastinae.

Achatinelloides Nevill, 1878	Mordan, 1986
Altenaia Zilch, 1972	Zilch, 1972
Amimopina Solem, 1964	Solem, 1964
Cerastus Albers, 1860	Hesse, 1933; Verdcourt, 1967; Verdcourt, 1970; Mordan, 1986
Conulinus Martens, 1895	Verdcourt, 1966
Edouardia Gude, 1914	Connolly, 1925; Verdcourt, 1970
Euryptyxis Fischer, 1883	Bourguignat, 1882; Mordan, 1986
Pachnodus Albers, 1860	Van Mol & Coppois, 1980
Rachis Albers, 1850	Seshaiya, 1932
Rhachistia Connolly, 1925	Tillier, 1989
Zebrinops Thiele, 1931	Bourguignat, 1882; Mordan, 1986

of *Edouardia* are recognised in the analysis: representatives of the smaller species are separated as one group, whilst the large, carinate species from southern Africa form the second.

The anatomy of the remaining seven genus-level groups within the Cerastinae is unknown. Of these, *Polychordia* Connolly from south-west Arabia is monotypic and is most probably synonymous with *Cerastus* Albers (Mordan, 1986), as is *Paracerastus* Thiele according to Verdcourt (1970: 18). *Limicena* Connolly and *Pleurorhachis* Connolly are both small groups with restricted ranges in Malawi, Zimbabwe and Mozambique, which are separated on the basis of highly distinctive protoconch sculptures. *Passamaella* Pfeiffer represents an endemic radiation of some seven species on the Indian Ocean island of Socotra (Smith, 1903).

Following Verdcourt (1983), it was originally believed that the dissected specimens of *histrio* Pfeiffer and *chiradzuluensis* E.A. Smith belonged to the genus *Rhachidina* Thiele. However, examination of the radula clearly showed that both belong to *Rhachistia* Connolly, and as a result *Rhachidina* also is unrepresented in the analysis.

Mabilliella Ancey is restricted to eastern Africa, but although the shell is superficially similar to *Cerastus*, it differs markedly in detail from any known cerastine; Verdcourt (1983: 216) included the only species, *Mabiliella notabilis* (E.A. Smith), in the family Subulinidae, and this genus is here excluded from the Cerastinae.

CHOICE OF OUTGROUP

Selection of the outgroup in phylogenetic analysis is of critical importance for it determines the polarity of many of the morphoclinal character-state changes used in the analysis. In an earlier paper (Mordan, 1984) I mentioned that it had proved difficult to establish clear synapomorphic characters to unite the Cerastinae with the northern subfamilies of Enidae. Since then, three important studies have been published addressing the problem of the interrelationships of the Orthurethra. Nordsieck considered the significance of the reproductive and excretory systems (Nordsieck, 1985) and subsequently the shell (Nordsieck, 1986). He afforded the cerastines full family status under the name Cerastuidae, but whereas in the earlier paper the Enidae (Buliminidae) were treated as Pupilloidea, in the later one they were united with the Cerastuidae to form the superfamily Buliminoidea. No justification for this relationship was given however.

Tillier (1989), in a major review of the Stylommatophora, included the Cerastinae as a subfamily of Enidae. His study was based principally on the nervous, alimentary and excretory systems and has revealed an important synapomorpy for the Enidae *sensu lato*, namely the extreme compaction of the visceral chain. In both the northern enids and the cerastines the left parietal ganglion is in contact with both the visceral and pleural ganglia. Tillier found that this character state correlated with large size, which in itself could be considered a further synapomorphy of the combined group. Additional indirect support for the use of the northern enids (Enidae *sensu stricto*) as the outgroup comes from Nordsieck (1985) who postulated the plesiomorphous condition of the orthurethran reproductive system, to which the Enidae conform very closely.

The endemic New Caledonian Draparnaudinae were included in the Enidae by Tillier (1989), following Solem (1962). However, implicit in Tillier's interpretation is the derived nature of the group, which makes them unsuitable for use as the outgroup in the present analysis. This is most obviously manifested in the simplified genitalia (a feature shared with the Partulidae), generally recognised to be the apomorphic state in the Orthurethra (Pilsbry, 1927; Nordsieck, 1985). The Draparnaudinae are currently being revised (Tillier & Mordan, in prep.).

If it is accepted that the northern Enidae represent the most likely sistergroup of the Cerastinae, the problem remains of which enid subfamily to select as outgroup. Forcart (1940) recognised two subfamilies, the Eninae and the Chondrulinae, based on the presence or absence of a penial appendix respectively. Nordsieck (1985) argued that the presence of a penial appendix is plesiomorphic, and as both the cerastines and enines possess such an appendix, it is more appropriate that the outgroup is selected from the Eninae; the type genus, *Ena* Turton, has been chosen as representative. Comparative anatomical information on the Eninae is based on Hesse (1933), Forcart (1940) and Shileiko (1984), as well as on new dissections.

FOSSIL AND RECENT DISTRIBUTION

Putative Enidae have been recorded from as long ago as the Carboniferous in North America and Europe (Solem & Yochelson, 1979), although the earliest records of a Recent genus is *Napaeus* from the Eocene of Europe (Zilch, 1959).

Fossil data on the Cerastinae are much more limited, and are derived exclusively from the Miocene of East Africa. Newton (1914) described a *Cerastus* from the Burdigalian at Karunga Bay, Kenya, which he referred to as *C.* cf. *moellendorffi* Kobelt, a species currently living in Ethiopia and Somalia. More recently, Verdcourt (1963) has described two new species of cerastine from Kenya: one a *Cerastus*, probably related to the Ethiopian and Somali group of species; the second provisionally placed by Verdcourt in *Edouardia*, but which he thought might alternatively be a *Rachistia*. The age of these fossils has now been confirmed as Burdigalian (Lower Miocene) by Dr Peter Andrews (personal communication) who has stated that Potassium/Argon dating ages these deposits at 18.0 ma BP. Other published information on the Cerastinae is restricted to some undated fossil *Euryptyxis* from fluviatile/aeolian deposits from south-western Arabia described by Wenz (1943); from the context of the paper the deposits are unlikely to be older than Quaternary, and all the fossils are referable to Recent species. The tentative inclusion of *Procerastus* Wenz of the Eocene of Europe in the Cerastinae (Zilch, 1959) should be treated with some caution. I have examined the types of *Partula dautzenbergi* Cossman, 1906 and whilst they do resemble cerastines in a number of features, principally the fine spiral sculpture, closed umbilicus, and overall shell shape, it is difficult either to exclude or include them with confidence.

Unlike the fossils, the Recent Enidae and Cerastinae have an entirely Old-World distribution. The northern Enids are essentially Palaearctic in range, but extend southwards into northern Africa, Arabia, India and Indonesia. In contrast, the Cerastinae have a present-day distribution throughout most of Africa, south-west Arabia, peninsular India, Sri

Lanka and northern Australia/south-east New Guinea (Fig. 1). In addition, endemic genera are to be found on the Indian Ocean islands of Socotra and the Seychelles, with representatives of a few genera occurring on the Western Indian Ocean islands such as Madagascar, Comores, Aldabra and the Mascarines, and into the Pacific. The only areas of distributional overlap between the cerastines and the northern Enidae are in south-west Arabia and parts of India and Sri Lanka (Mordan, 1984).

The distributions of those genera excluded from the cladistic analysis have already been discussed above. Of those utilised in the analysis, *Rhachistia* has a widespread distribution in Africa south of the Sahara, and extends to Madagascar, India, Sri Lanka and numerous islands of the Indo-west Pacific. A single species, *Rachistia histrio*, appears recently to have spread to a number of Pacific Ocean islands such as the Celebes, New Caledonia and New Hebrides (Verdcourt, 1983). *Rachis* and *Edouardia* have similar continental distributions to *Rhachistia* occurring widely in Africa and India, but both have rather less extensive ranges in the Indian Ocean and are absent from the western Pacific. *Altenaia* is the only exclusively West African genus, being restricted to Angola and Namibia (Zilch, 1972).

Cerastus extends from northern Ethiopia and south-west Arabia down as far as northern Mozambique, and wetwards into the Congo. This genus also occurs in western India from Kutch in the north as far south as Malabar, but is absent from Oman (Mordan, 1986), although the type species, *Cerastus distans* (Pfeiffer), has Karah Island in the Arabian Gulf as its type locality. *Euryptyxis* and *Zebrinops* have similar distributions in Ethiopia, Somalia and south-west Arabia. In addition there are endemic radiations in the Seychelles (*Pachnodus*) and on Socotra (*Achatinelloides* and *Passamaella*). *Conulinus* is a small group of four species with a restricted range in East Africa (Verdcourt, 1966).

Amimopina has perhaps the most interesting distribution of all, occurring in northern Australia and south-eastern New Guinea. In Australia it extends right round the north of the continent from North-west Australia across to Queensland as far south as Proserpine (John Stanisic. *in litt.*). It is possible, however, that this genus is more widespread than previously thought, as the type series of *Bulimus subangulatus* Pfeiffer from Cambodia has recently been isolated (BMNH Reg. No. 1986166) and appears to be extremely close conchologically to topotypic material of *Amimopina beddomei* Brazier. The published type locality for the two syntypes of

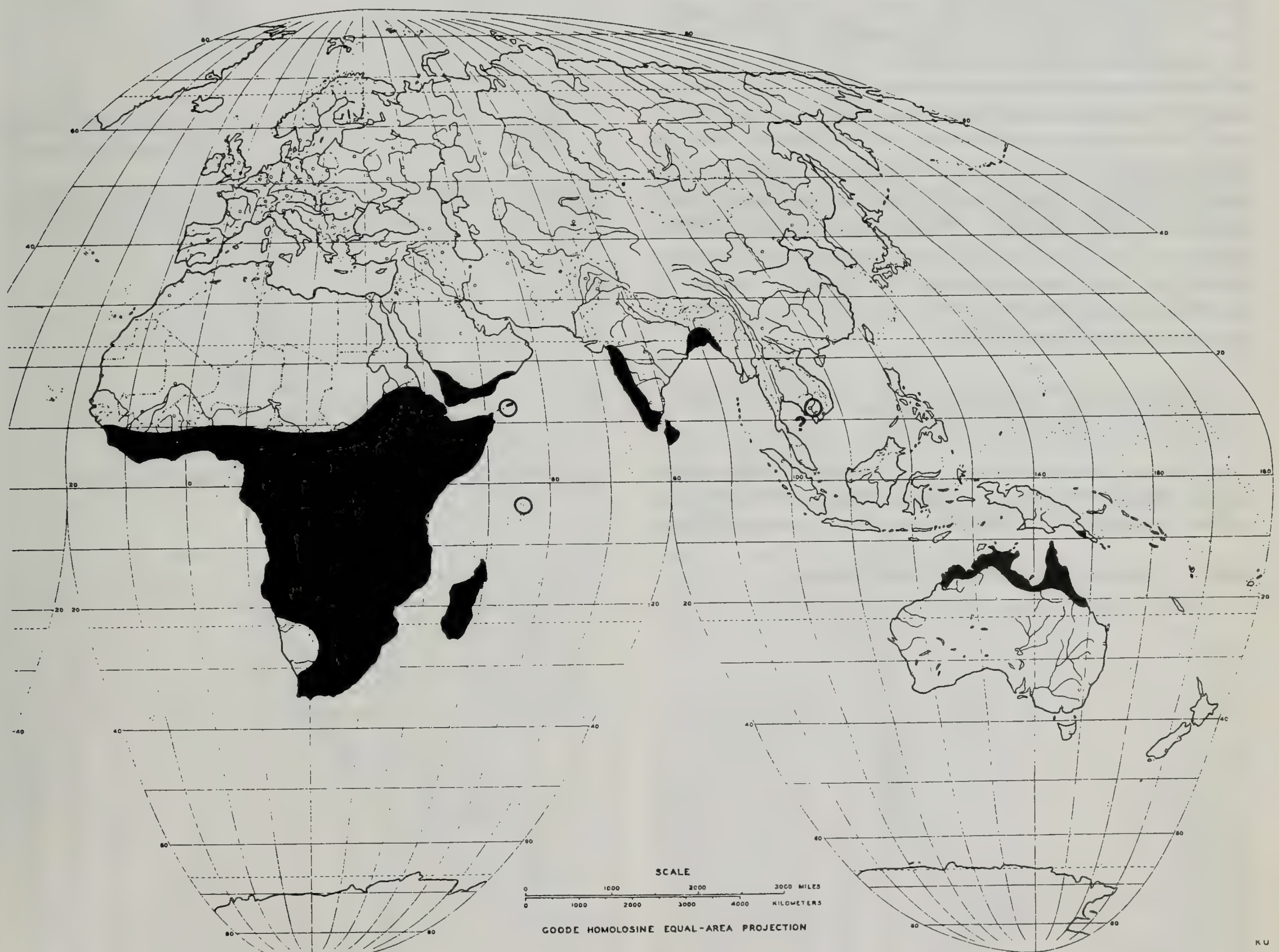
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Fig. 1 Map showing continental distribution of the Cerastinae. Circled areas include the 'continental' islands of Socotra and the Seychelles, and also the questionable record of *Amimopina* in Campuchia. Distribution is not necessarily continuous throughout the marked areas.

Table 2 Character states used in phylogenetic analysis

1. Renal fold absent (0); present (1); closed (2).
2. Rectal fold absent (0); present (1); reduced (2).
3. Spermathecal stalk long (0); short (1).
4. Internal epiphallar ornamentation folds (0); Pits (1).
5. Base of central stalk of penial appendix thickened (0); not thickened (1).
6. Base of central stalk of penial appendix uncovered (0); ensheathed (1).
7. Appendicular retractor muscle inserting on basal portion of appendix (0); inserting on central stalk (1).
8. Penial and appendicular retractor muscles with joint origin (0); separate origin (1).
9. Penial retractor muscle inserting on penis (0); epiphallus (1); penis and epiphallus (2).
10. Penial caecum absent (0); elongate and well defined (1); rounded and poorly defined (2).
11. Penial pilasters/glandular pads symmetrical (0); asymmetrical (1).
12. Penial flagellum absent (0); present (1).
13. Genital atrium unpigmented (0); pigmented (1).
14. Tail crest absent (0); present (1).
15. Background shell colour dark (0); light (1).
16. Shell unpatterned (0); patterned (1).
17. Shell lip present (0); absent (1).
18. Columellar fold absent (0); present (1).
19. Umbilicus closed (0); open (1).
20. Radular row shape weakly arcuate (0); marginals angled back (1); laterals and marginals angled forwards (2).
21. Lateral teeth pointed (0); blunt (1).
22. Central tooth with ectocones (0); without (1).

subangulatus is 'Lao Mountains, Camboja' collected by Mr Mouhot. As the paper in which *Bulimus subangulatus* was originally described (Pfeiffer, 1862) included numerous other species from the same locality and collector, these data are unlikely to be in error although the possibility cannot be excluded. It must also be stressed that the soft anatomy of *subangulatus* remains unknown.

ANATOMICAL CHARACTERS

The analysis is based primarily on the anatomy of the pallial and reproductive systems, but also includes several shell and radular characters. The cerastine excretory system exhibits a

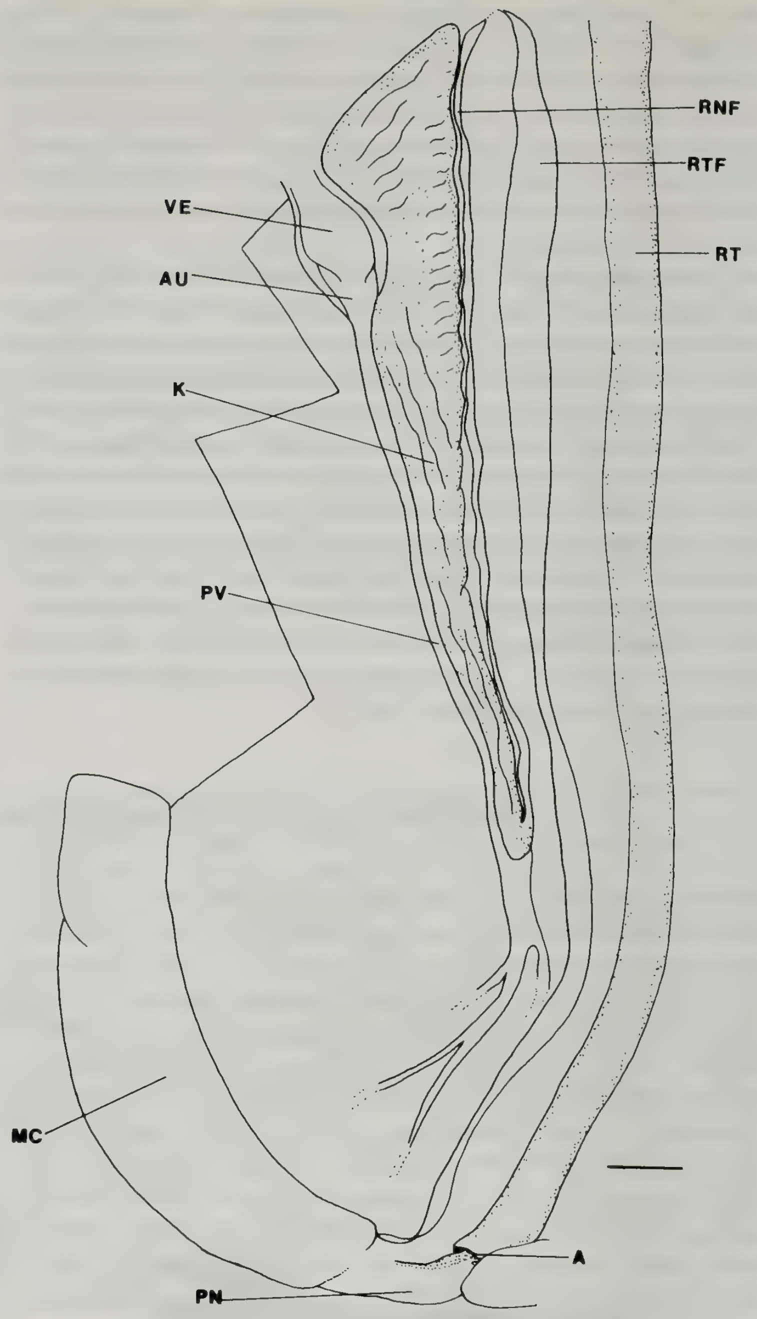

Fig. 2 *Cerastus trapezoidea*, Kitale, Kenya. Scale line 2 mm.

Table 3 Character state matrix of cerastine genera.

	Character																					
Genus	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22
Ena	0	0	0	0	0	0	0	9	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Rachis	1	1	0	1	1	1	0	0	1	1	0	0	1	0	1	1	1	0	1	0	0	0
Conulinus	1	1	0	1	0	1	0	0	1	1	0	0	1	1	0	0	1	0	1	0	0	0
Zebrinops	1	1	0	1	1	1	1	1	1	1	0	0	1	0	1	1	1	0	1	0	0	0
Cerastus	1	1	0	1	0	1	1	0	1	1	0	0	9	1	0	0	0	0	1	0	0	0
Pachnodus	1	1	0	1	0	0	0	0	1	0	0	0	1	1	0	9	0	0	1	1	1	1
Euryptyxis	1	1	0	1	9	0	0	1	1	1	0	0	1	0	1	0	0	1	0	0	0	0
Achatinelloides	1	1	0	1	1	0	0	1	1	1	0	0	1	0	1	1	1	1	0	0	0	0
Rhachistia	2	9	1	0	0	0	0	9	0	2	1	1	1	0	1	1	1	0	1	2	1	1
Edouardia (small)	2	0	1	0	0	1	0	0	2	2	1	1	1	0	0	0	1	0	1	0	0	1
Edouardia (large)	2	2	1	0	0	1	0	0	2	2	1	1	1	0	0	9	1	0	1	0	0	1
Amimopina	2	1	1	0	0	0	0	0	2	2	1	1	1	0	0	0	1	0	1	2	1	1

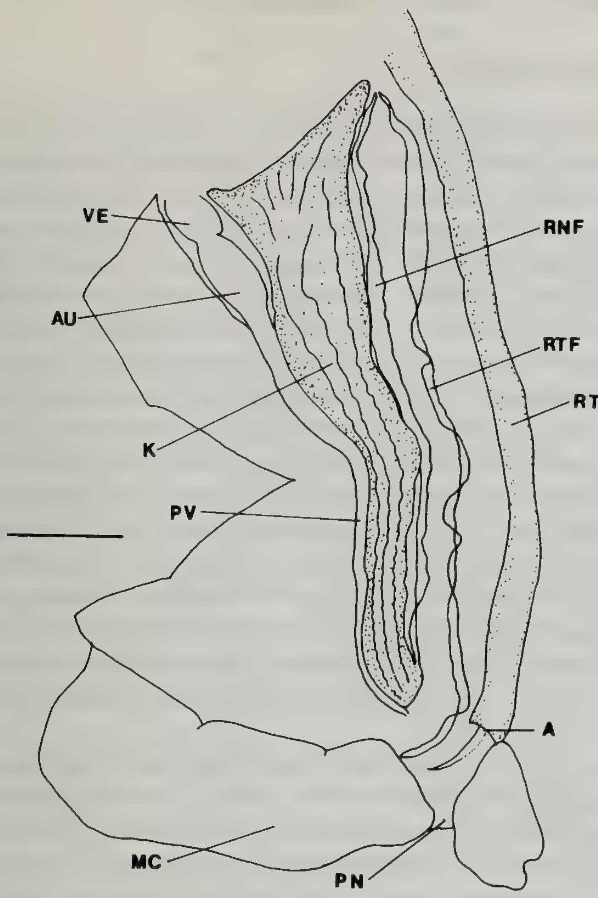

Fig. 3 Pallial complex, *Conulinus rutshuruensis*, Thika, Kenya. Scale line 2 mm.

number of new structures which themselves show a range of variation within the group, whilst the genital systems of the Arabian cerastines studied by Mordan (1986) were found to provide many useful taxonomic characters at the generic level. One external character, termed the tail crest, is also utilised as it is clearly restricted to certain genera. Table 1 lists the principal published sources of information on the anatomy of cerastines.

In choosing the characters to be used in the phylogenetic analysis (Table 2), two further factors were borne in mind: all characters autapomorphic at the generic level were excluded as these cannot contribute to the structure of the tree; secondly, it was decided not to include fully correlated characters where these appeared to be functionally related to an already coded character, as this would tend artifically to increase the consistency index of the tree (Reid, 1989).

Pallial Complex (Characters 1–2)

The excretory system of the Cerastinae exhibits a greater degree of elaboration than any other orthurethran group. In many orthurethrans, including the Enidae, a weakly developed ridge is found extending from the renal orifice along the side of the kidney to form a backwardly directed ‘gutter’, but in all cerastine genera a complete renal fold is developed, running the entire length of the kidney to the top of the lung cavity (Character 1). With the exception of certain small *Edouardia*, an additional fold runs downwards from a point of junction with the renal fold at the top of the lung, along the rectum as far as the pneumostome; this is termed the rectal fold (Character 2) and is not known from any other Orthurethra. In the region of the pneumostome the fold flexes away from the base of the rectum and tapers to a ridge, finally fusing with the inner wall of the mantle collar (van Mol & Coppois, 1980, Fig. 2; Mordan, 1986, Fig. 29b). A similarly

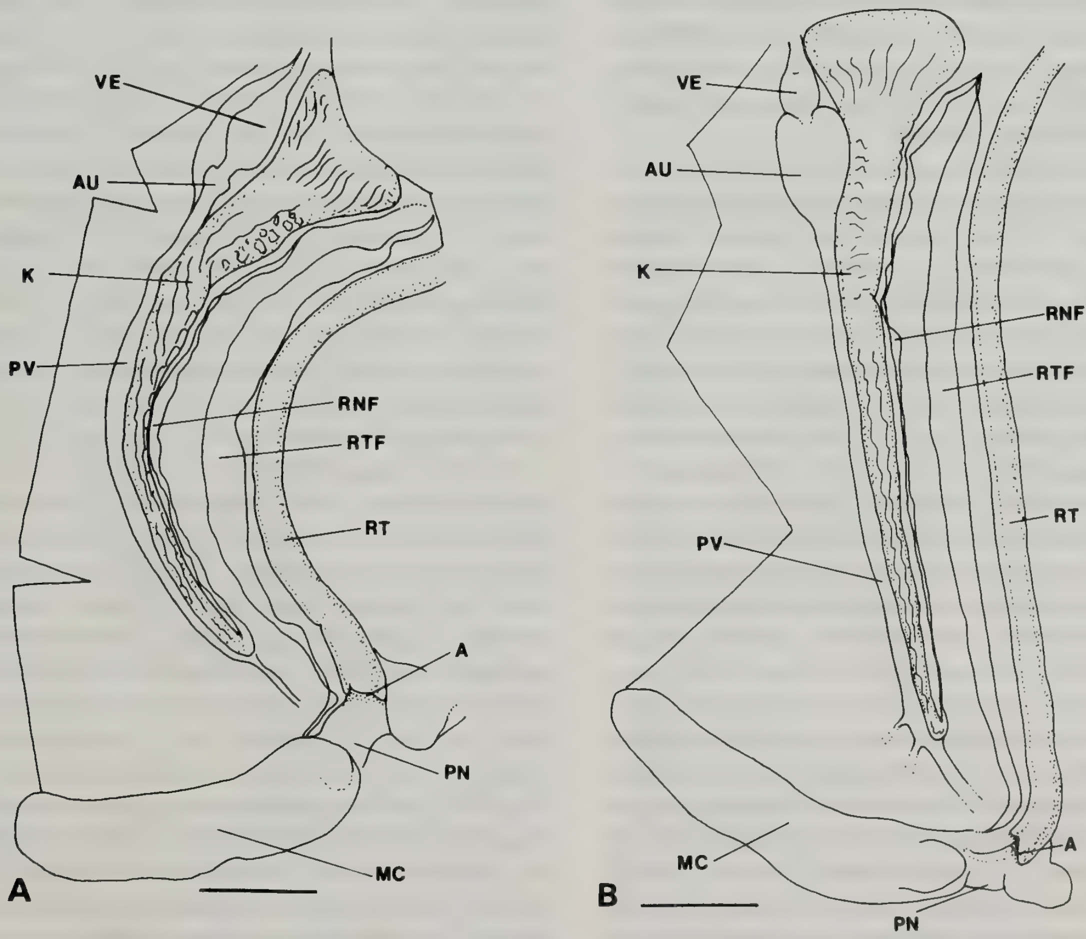

Fig. 4 Pallial complex. A. *Rachis punctata*, Dar es Salaam, Tanzania; B. *Achatinelloides socotrensis*, Socotra. Scale lines 2 mm.

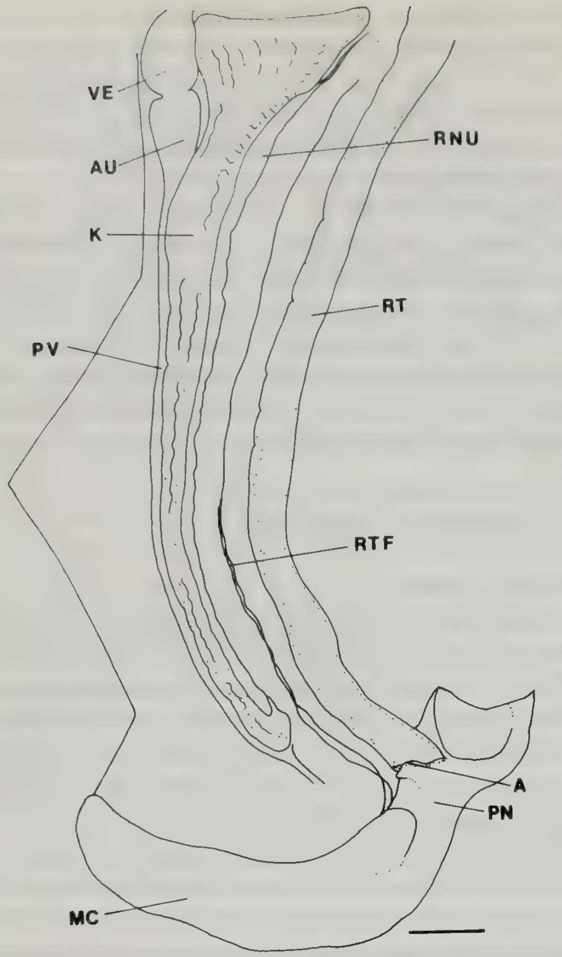

Fig. 5 Pallial complex, *Rhachistia rhodotaenia*, Nairobi-Mombassa Road, Kenya. Scale line 2 mm.

positioned and shaped pneumostomal ridge is also found in many other orthurethran families (Tillier, 1989). This arrangement of renal and rectal folds is already known from such cerastine genera as *Euryptyxis, Zebrinops* (Mordan, 1986) and *Pachnodus* (van Mol & Coppois, 1980), but is here figured also in *Cerastus* (Fig. 2), *Conulinus* (Fig. 3), *Rachis* (Fig. 4A) and *Achatinelloides* (Fig. 4B).

In a number of cerastine genera, the renal fold is fused to the kidney to form a tube—a feature first described in *Amimopina* by Solem (1964: Fig. 1) who termed it the 'pseudosigmurethrous' condition. A similar arrangement is found in *Rhachistia* (Figs 5, 6; Tillier, 1989: Fig. 137), and has also been confirmed in *Edouardia* (Fig. 7). Normally this is fused along almost its entire length to form a closed ureter, but in *Edouardia natalensis* fusion only extended about half way up the length of the kidney (Fig. 8). The presence of the pseudosigmurethrous condition is considered to be apomorphic to the possession of an unfused fold following the arguments of Tillier (1989), and consequently character 1 is ordered for the purposes of the analysis. In some species of *Rhachistia* the upper part of the rectal fold is reduced (Figs 5, 6B), although a thin ridge of tissue remains visible, and in *Edouardia* cf. *metula* (Fig. 7) it appears to be entirely missing.

Two further characteristics of the cerastine pallial complex should be noted, but were not utilised in the analysis. The prominent pallial venation, which is present in all genera, is correlated with the development of pallial folds and is thought to be a result of lung shortening (Tillier, 1989). Secondly, a well-developed mantle gland, characteristic of the northern Enidae (Mordan, 1984), was not found in any of the cerastines examined.

Reproductive System (Characters 3–13)

Penis and Epiphallus

The enine penial complex appears to be fairly uniform in structure and that of *Ena* is typical. The epiphallus enters the penis apically and the two regions are not always distinguishable externally, excepting that the top of the penis may become expanded where it contains a penial papilla. No penial caecum is present, although a structure termed the caecum does occur on the epiphallus, as does a short terminal flagellum; both are concerned with the shaping of the spermatophore (Schikow, 1978), and should not be confused with the homonymous (but not homologous) structures on the cerastine penis. Internally, both the penis and epiphallus have predominantly longitudinal pilasters. All enines possess a penial appendix of the typical orthurethran type. The basal portion of the appendix opens laterally onto the lower part of the penial tube, and also receives the insertion of the appendicular retractor muscle. The penial retractor inserts onto the top of the penis. These two muscles originate separately on the lung wall in *Ena*, but they are joined in many other enines.

The penis of the Cerastinae differs from that of the Eninae in a number of significant respects, perhaps the most obvious being the presence of a well-developed caecum in all but one genus. Two principal cerastine penial types occur. The more restricted of the two, referred to as the flagellate type, is known in *Amimopina* (Fig. 9; Solem, 1964: Fig. 2), *Edouardia* (Figs 10, 11; Verdcourt, 1967, Fig. 25), and *Altenaia* (Zilch, 1972: Fig. 5), and is also figured here from *Rhachistia* (Figs 12, 13). The penial flagellum (Character 12) is an elongate, blind-ended sac inserting on the head of the penis close to the point of entry of the epiphallus. The penial flagellum varies greatly in length; it may be as short as the penis itself or, as in *Rhachistia* and some *Edouardia*, about as long as the penial appendix. A penial caecum (Character 10) is developed in these genera but shows little differentiation internally from the rest of the penis. There are weak longitudinal pilasters in the main stem of the penis, but within the expanded apical region is a transverse glandular patch (Character 11) which is fairly extensive in *Rhachistia rhodotaenia* and *Edouardia* (Figs 14A, 15A, 16C), rather weaker in *Amimopina* (Fig. 17A) and reduced to a simple, tapering ridge in *Rhachistia histrio* (Fig. 18A). The penial retractor muscle inserts on the penis and insertion is often multiple; in *Edouardia* and *Amimopina* (Figs 15A, 17C) a lateral branch to the epiphallus was noted (Character 9).

All the remaining cerastine taxa considered here lack a penial flagellum. With the single exception of *Pachnodus*, the penis possesses a well-developed, often pointed caecum (*eg. Rachis* and *Achatinelloides*, Fig. 21), and epiphallar insertion onto the penis is more clearly lateral. Longitudinal penial pilasters are also normally better developed in this group than in flagellate forms, and usually expand apically into large, symmetrically paired, glandular patches within the caecum. The limit of the caecal area is normally distinguishable internally by a change in ornamentation (eg. *Cerastus*, Fig. 19B) or the presence of a circular ridge (*Conulinus*, Fig. 20C). As mentioned above, *Pachnodus* has no caecum, the epiphallus being continuous with the top of the penis, with no visible external demarcation between the two regions (Fig. 22A; van Mol & Coppois, 1980).

In all Cerastinae a sheath of muscle encircles the stem of

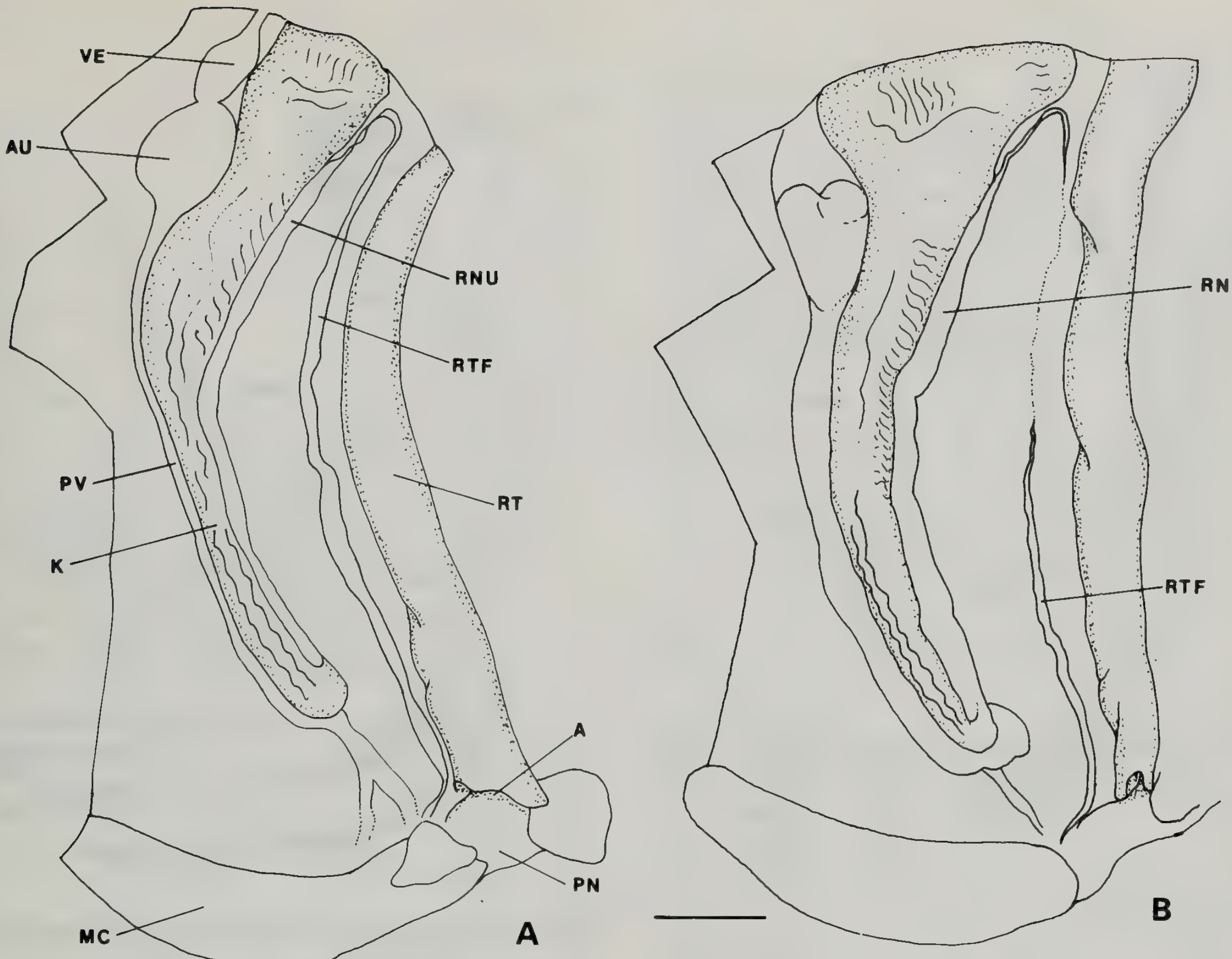

Fig. 6 Pallial complex; A. *Rhachistia chiradzuluensis*, Thika, Kenya; B. *Rhachistia histrio*, Maré, Loyalty Islands. Scale line 2 mm.

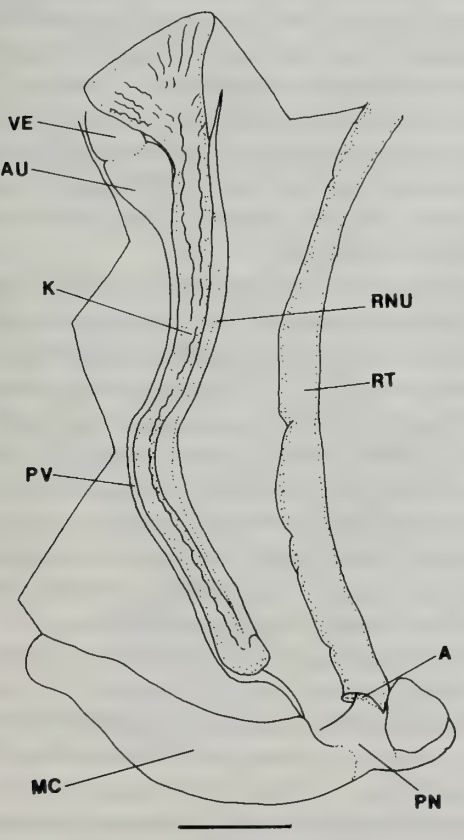

Fig. 7 Pallial complex, *Edouardia* cf. *metula*, Nairobi, Kenya. Scale line 2 mm.

the penis above the level of appendicular insertion. This is only attached at one end but may be directed upwards (eg. *Rachis*, Fig. 23A; *Pachnodus*, van Mol & Coppois, 1980, Fig. 5) or downwards (eg. *Rhachistia*, Fig. 18A; *Conulinus*, Fig. 20C) from the point of attachment. In some cases the downwardly directed muscle is recurved to form a double-layered structure (eg. *Cerastus*, Fig. 19B; *Achatinelloides*, Fig. 24A). The arrangement appears to be constant within species but, on the evidence of *Euryptyxis*, may vary between congeneric species (Mordan, 1986). The sheath is generally weaker in flagellate genera, and in *Edouardia* (Fig. 15A) is barely visible, being extremely fine, single-layered, and closely adpressed to the wall of the penis. As the sheath was found in all cerastine taxa, it was not utilised in the analysis.

The form of the cerastine epiphallus (character 4), and hence of the spermatophore which it secretes, is broadly correlated with penis type. Flagellate groups such as *Edouardia* (Figs 10, 11) and *Rhachistia* (Figs 12, 13), have an externally simple epiphallar region, only distinguishable from the vas deferens by the greater thickness of the former. Internally, the epiphallus is ornamented with longitudinal, sometimes spiral folds which in the case of *Rhachistia rhodotaenia* appear to correspond to the pair of fins which extend along about half the length of the spermatophore (Figs 14B, 25). In this species the fin becomes finely serrated along part of its length, as in some Eninae (Schikow, 1978). In contrast, the non-flagellate taxa have a spermatophore characterised by a longitudinal row of strong, discrete, hooked spines which may bear forked or complex digitiform terminations (Hesse, 1933, Fig. 43e; Mordan, 1986, Fig. 24c). The elaborate structure required to mould these spines is visible externally as a series of transverse ridges on the epiphallus (Figs 20B, 22A, 23D, 24A) and internally as a row of pits (Figs 19A, 20A,

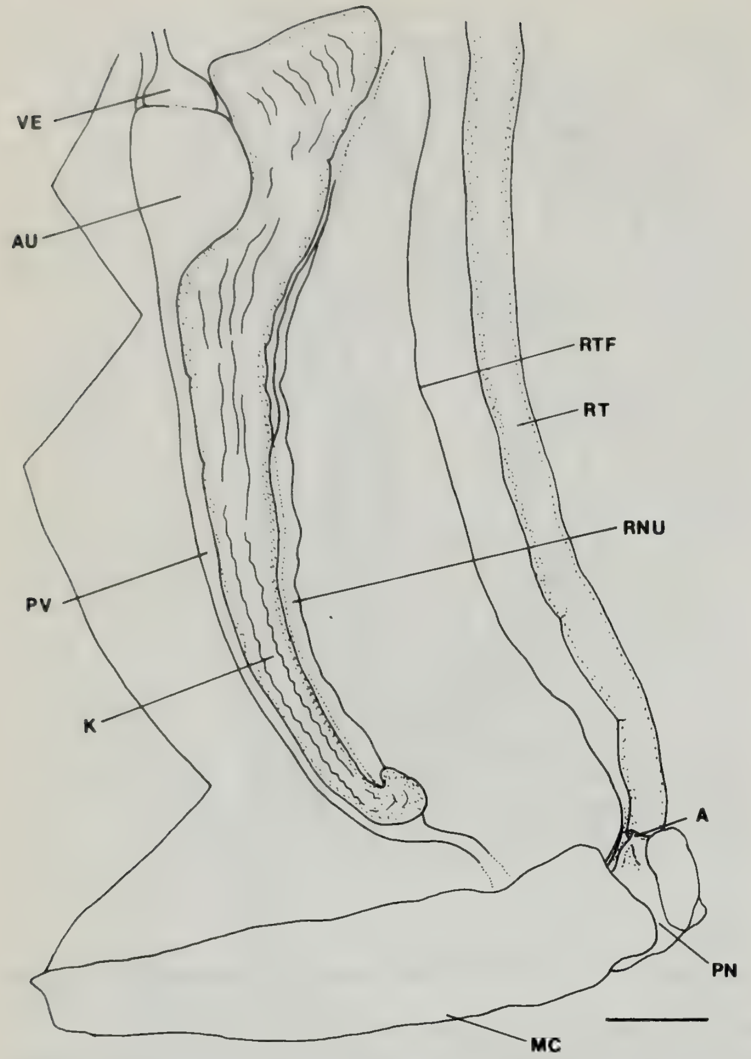

Fig. 8 Pallial complex, *Edouardia natalensis*, Pietermaritzberg, South Africa. Scale line 2 mm.

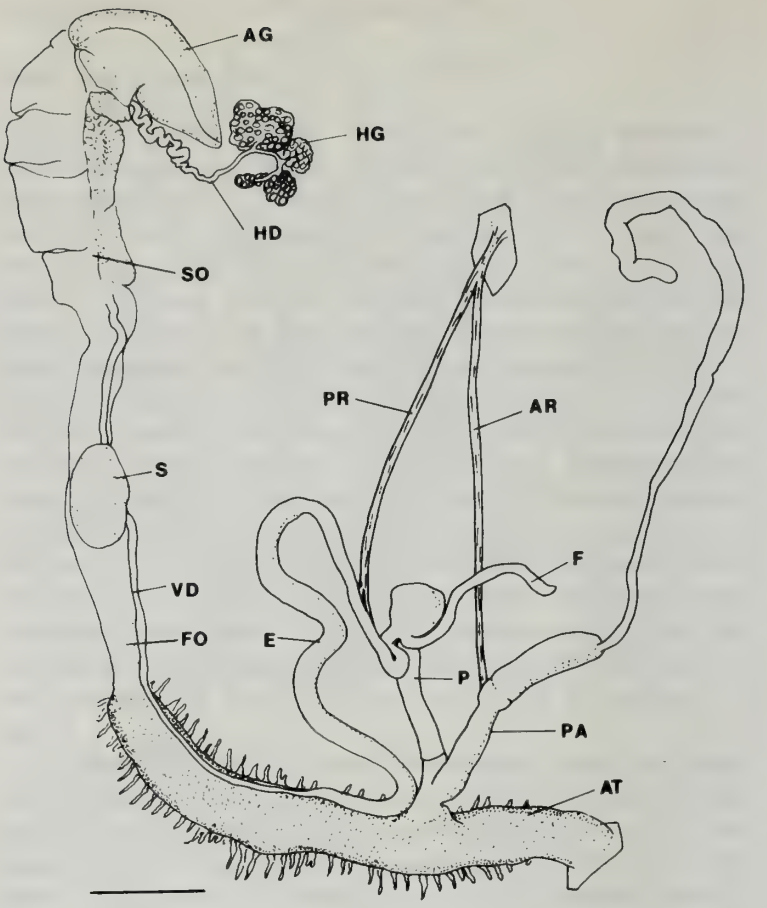

Fig. 9 Genital system. *Amimopina macleayi*, Daly River, Australia. Scale line 2 mm.

22C, 23B, 24B) which correspond in number precisely to the number of spines on the spermatophore (Mordan, 1986). In those non-flagellate taxa where even quite major modifications in spermatophore structure have taken place, such as species of *Pachnodus sensu stricto*, vestigial hooks remain (van Mol & Coppois, 1980: Figs 11; 12)

Penial appendix

A penial appendix of the typical orthurethran pattern occurs in all cerastines which have been dissected. Three principal regions of this appendix may be recognised: a wide, eversible, basal portion proximal to the penis, onto which it inserts laterally below the penial muscle sheath close to the atrium; a much narrower, thick-walled, central stalk; and an elongate terminal bulb. Shileiko (1979) has distinguished five regions by including areas of differentiation at the junction of the basal region with the central stalk (Characters 5–7), and certainly it is this particular area of the appendix which shows perhaps the greatest variation between genera, and is therefore of much taxonomic interest. Three basic structural patterns occur in this region within the Cerastinae, and these are diagramatically represented in Fig. 26.

The simplest type (Fig. 26C) is that found in *Achatinelloides* (Fig. 24C), most *Euryptyxis* (Mordan, 1986), and apparently also in some *Pachnodus* (van Mol & Coppois, 1980: Figs 5, 6), where there is a straight insertion of an undifferentiated central stalk onto the base. There may be a slight papilla at the point of entry of the stalk and a weak ring pilaster around the top of the basal lumen, and in some species belonging to the last two genera the base of the stalk may be somewhat thickened (Mordan, 1986, Fig. 23). In all three genera the appendicular retractor muscle inserts at, or just below the top of the basal portion of the appendix, although in *Euryptyxis* the muscle embraces but does not enclose the base of the central stalk prior to insertion (Mordan, 1986: Figs 30, 31b).

The second appendix type (Fig. 26D), already noted above as occurring in one species of *Euryptyxis* and some *Pachnodus* (Fig. 22B), is characteristic of *Rhachistia* (Figs 14C, 18A, D) and *Amimopina* (Fig. 17A) and possibly also *Altenaia* (Zilch, 1972: Fig. 5). Here the muscular wall of the central stalk becomes heavily thickened at its base (Character 5), the retractor again inserting at or below the top of the basal region. This is the condition found in the Eninae, and is also widespread in the Orthurethra, and is therefore considered to be the primitive state. As before, a weak papilla may protrude into the lumen of the appendix base.

In the remaining genera a thin muscular sheath actually encloses the base of the stalk (Character 6; Fig. 26A, B). Within this category there are differences in the position of the retractor muscle insertion (Character 7): *Cerastus* (Fig. 19C), and less obviously *Zebrinops* (Mordan, 1986: Fig. 37D), have the appendicular retractor inserting onto the top of the sheath (Fig. 26A), but in *Rachis* (Fig. 23C), *Conulinus* (Fig. 20D, E), and *Edouardia* (Figs 15C, 16B, C) the retractor muscle is situated in the more-usual position at or below the top of the basal region (Fig. 26B). The enclosed region of the central stalk may become elaborated internally (Figs 15C; 19C; 20D, E), and may project into the lumen of

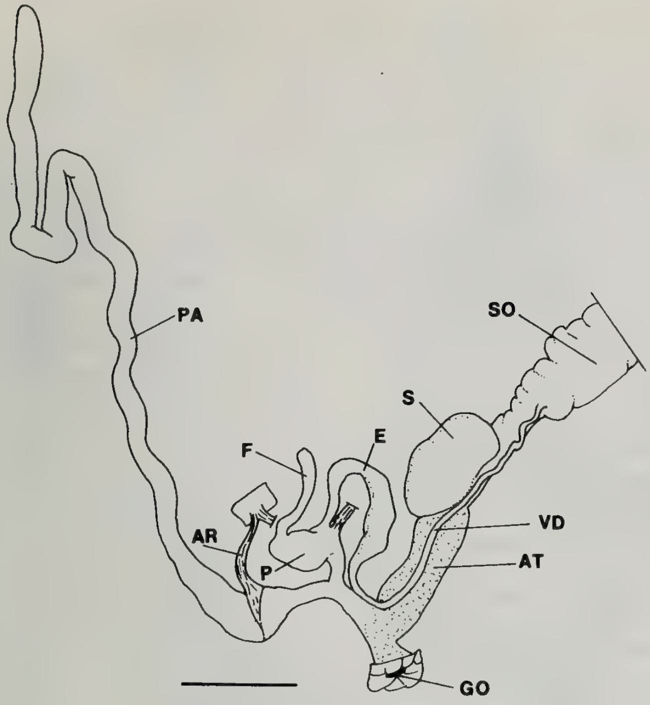

Fig. 10 Genital system. *Edouardia tumida*, Mombassa Island, Kenya. Scale line 2 mm.

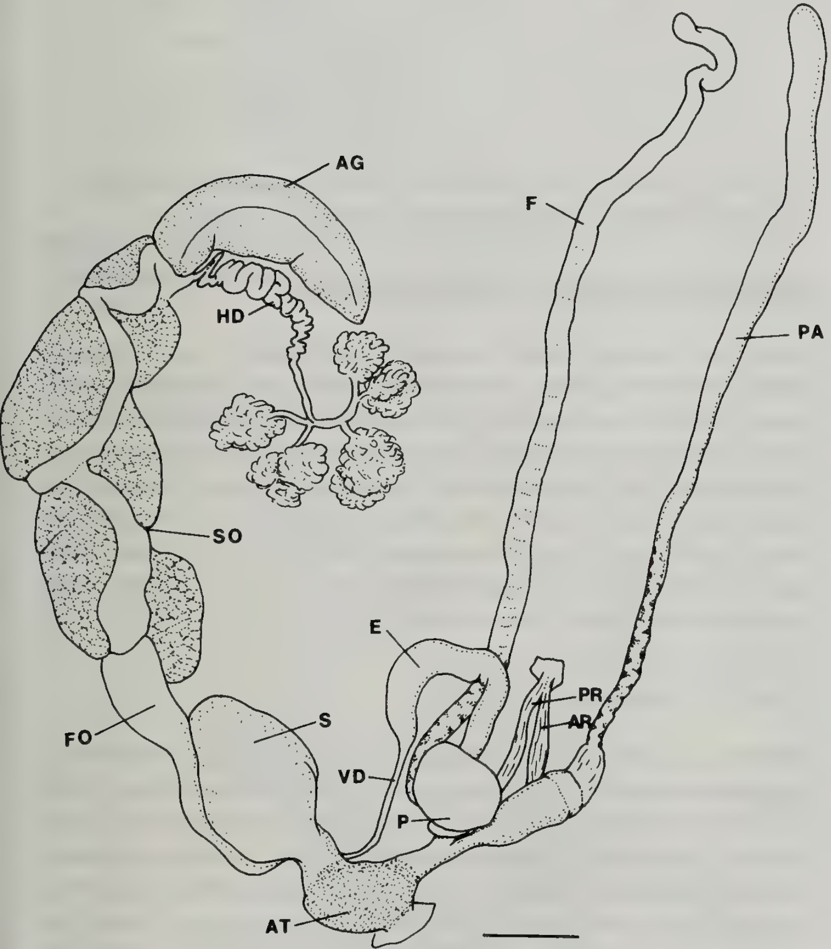

Fig. 11 Genital system. *Edouardia natalensis*, Pietermaritzberg, South Africa. Scale line 2 mm.

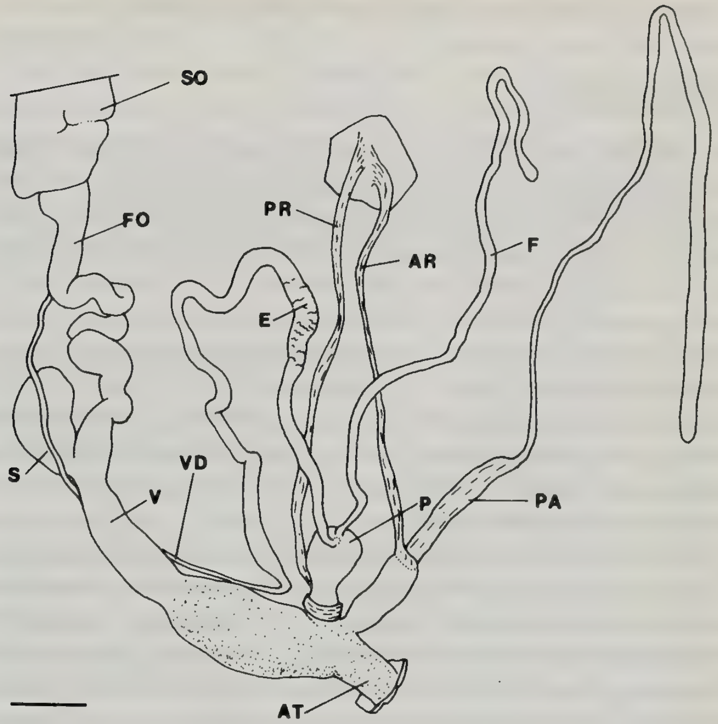

Fig. 12 Genital system. *Rhachistia rhodotaenia*, Nairobi-Mombassa Road, Kenya. Scale line 2 mm.

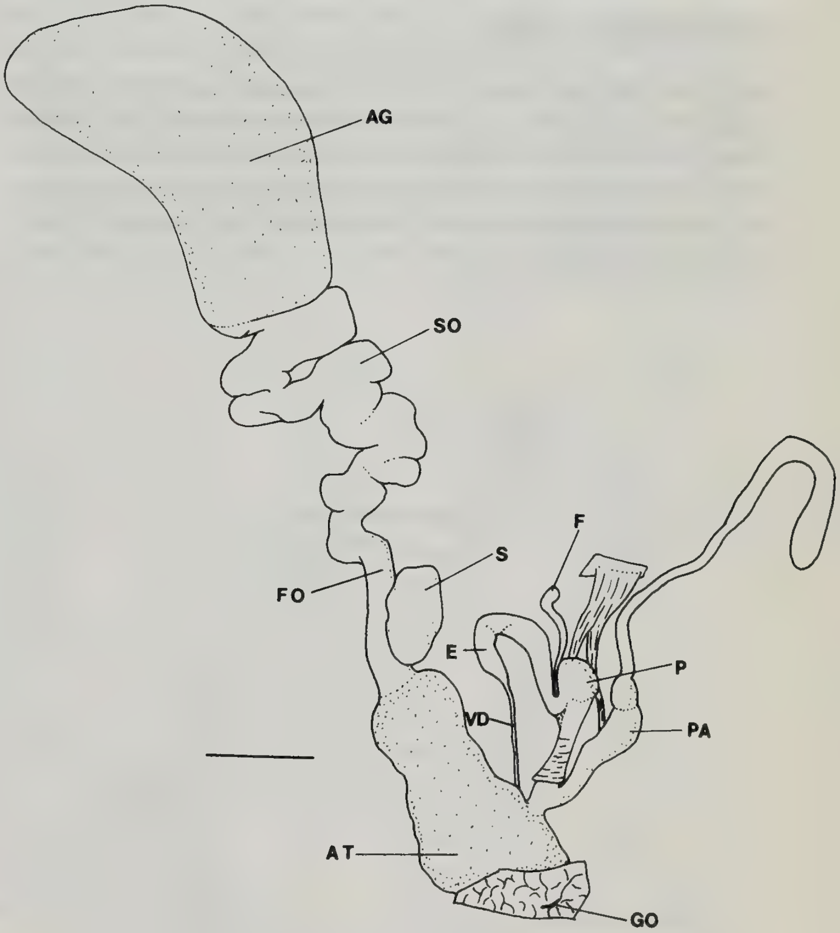

Fig. 13 Genital system. *Rhachidina histrio*, Maré, Loyalty Islands. Scale line 2 mm.

the base as a prominent papilla (*eg*. Fig. 20D). Throughout the group there is considerable variation in the extent of papillar development within species. However, this would appear to be related in large part to the degree of relaxation of the preserved specimen and thus of limited taxonomic value.

Both the appendicular and penial retractor muscles (Character 8) originate on the lower lung wall (diaphragm). In most genera (eg. *Amimopina*, Fig. 9; *Rachis*, Fig. 21A) they are joined from their origin over a considerable part of their length, whilst in others they are entirely separate (eg. *Achatinelloides*, Fig. 21B). In most enines, including *Ena*, the muscles are separate but in some they are joined. This character is thus scored as being variable for the Eninae.

Female system

The female part of the reproductive system generally shows far less variation between genera than does the male, but two features are of particular significance in respect of the Cerastinae. A highly characteristic brown spongy tissue lines the atrium and part of the vagina (Seshaya, 1932; Solem, 1964), and apparently is unique to the group (Character 13). It was present in all cerastines examined excepting *Cerastus trapezoidea* from east Africa. Its absence from certain African *Cerastus* of the *bambuseti* group to which *C. trapezoidea* belongs, has already been noted by Verdcourt (1967; 70). Histological details of this tissue in *Pachnodus* are given by van Mol & Coppois, 1980.

A second feature of interest is the form of the spermatheca (Character 3). This falls into two categories which correlate with penis structure. In genera with a flagellate penis the spermatheca lacks an obvious stalk (*Edouardia*, Figs 10, 11; *Rhachistia*, Figs 12, 13; *Amimopina*, Fig. 9; *Altenaia*, Zilch, 1972: Fig. 5), whilst in the remaining genera a clearly defined stalk or peduncle is present (*eg*. Fig. 21A, B). A spermathecal diverticulum, such as is found in many northern enid genera, has not been recorded in any Cerastinae.

Hermaphrodite system

Northern Enidae *sensu stricto* are characterised by the presence of hermaphrodite duct diverticulae (Mordan, 1984; 1986), but careful examination has not revealed these structures in any cerastine. In all cases the talon was a simple fold in the hermaphrodite duct, as recorded by Mordan (1986: Fig. 36A) for *Zebrinops*.

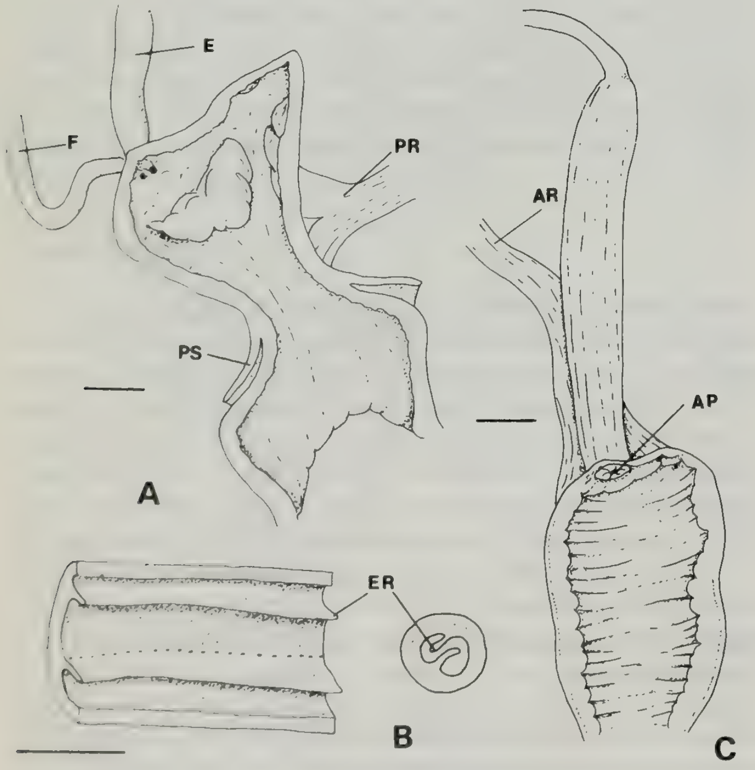

Fig. 14 A. Penis; B. Epiphallus; C. Penial appendix. *Rhachistia rhodotaenia*, Nairobi-Mombassa Road, Kenya. Scale lines 0.5 mm.

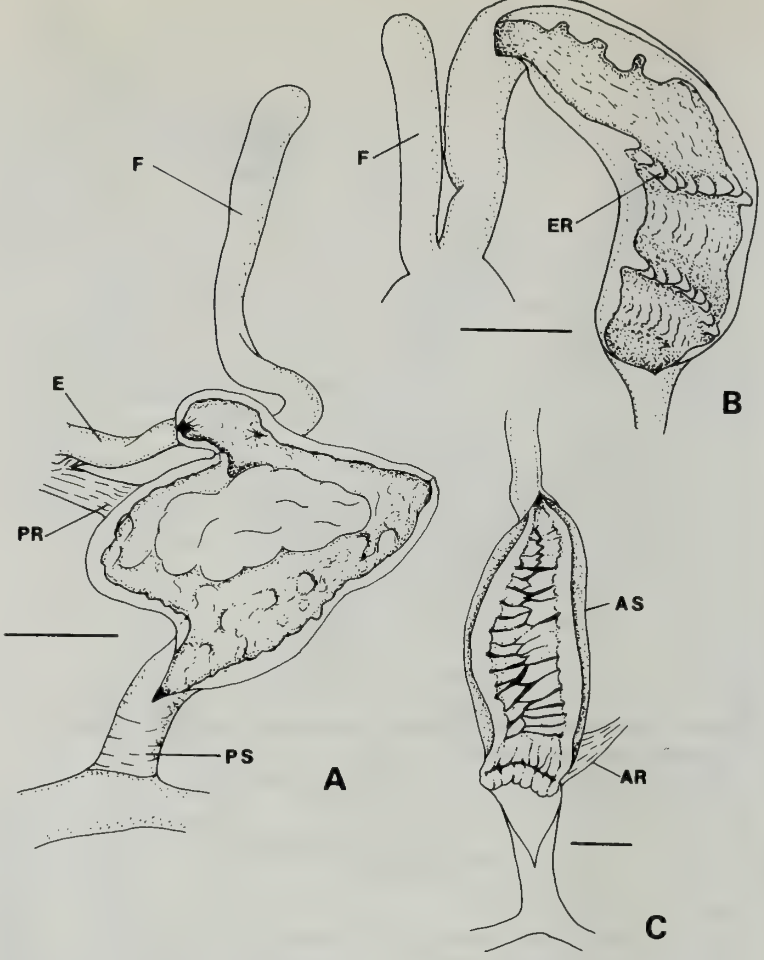

Fig. 15 A. Penis; B. Epiphallus; C. Penial appendix. *Edouardia tumida*, Mombassa Island, Kenya. Scale lines 0.5 mm.

External Features (Character 14)

Only one external body character was found to vary consistently between genera: the development of a prominent tail crest. This is situated along the dorsal mid-line of the tail and comprises a row of pointed tubercles, which are often paler in colour than the rest of the tail. The crest is clearly evident in *Cerastus, Conulinus* and *Pachnodus* (Fig. 27B–D) but not in other cerastines (eg. *Edouardia*, Fig. 27A). It does not appear to have been noted previously in the Cerastinae, nor indeed in any other orthurethran.

Shell (Characters 15–19)

Whilst most shell characteristics are, in general, remarkably consistent within cerastine genera, both size and shape are too variable to be of value in the analysis. Background shell colour (Character 15) tends either to be pale cream or brown, depending to some extent upon the thickness of the periostracal and calcareous layers. Similarly, entire genera have the propensity to develop patterning (Character 16), whereas others never do. This patterning typically takes the form of up to five spiral bands which may become broken up and fused to form a variety of characteristic patterns. These are particularly pronounced in *Rachis, Rhachistia* and *Rhachidina*, which have long been confused taxonomically, as well as in *Achatinelloides* and *Zebrinops*. Some species of *Pachnodus* and *Edouardia* develop a single, peripheral band but in both genera, species with an unpatterned shell are by far the more usual.

A lip (Character 17) only develops on the adult shell, and genera were readily classified as lip present or absent. In most genera the umbilicus (Character 19) remains open, although it can vary from widely gaping (eg. *Conulinus*) to minute (eg.*Rhachistia*), but in *Euryptyxis* and *Achatinelloides* it becomes closed off. These last two genera additionally develop a columellar fold or ridge (Character 18) which is clearly visible in the aperture, and which may become considerably enlarged further back within the body whorl (Mordan, 1986).

Radula (Characters 20–22)

In separating the Cerastinae (or Pachnodinae) from the northern Enidae, Watson (1920: 23) noted that in many cerastine species 'most of the teeth of the radula, instead of having their major axes practically in a line with one another, are placed more or less obliquely, so that the outer side of one tooth is in front of the inner tooth next beyond'. In *Pachnodus* (van Mol & Coppois, 1980) there is a clear backward angulation of the marginal teeth relative to the laterals, which lie in a relatively straight row. By way of contrast, in all eleven species of *Rhachistia* and one of *Amimopina* whose radulae were examined in the present study, the entire row is angled forward in a V shape from the central tooth at a fairly constant angle of about 110°. Both these patterns are distinct from the weakly arcuate row form characteristic of the remaining cerastine genera and the Eninae (Mordan, 1986: Fig. 19e). Thus three states of radular row pattern are recognised in the analysis (Character 20). In most of the cerastines examined, tooth form is fairly uniform: the central mesocone is pointed and bears a pair of smaller ectocones; laterals have a similarly pointed mesocone with well-developed ectocone but no endocone; and the marginals carry blunt, rounded mesocones and ectocones broken up into a series of pointed cusps which becom

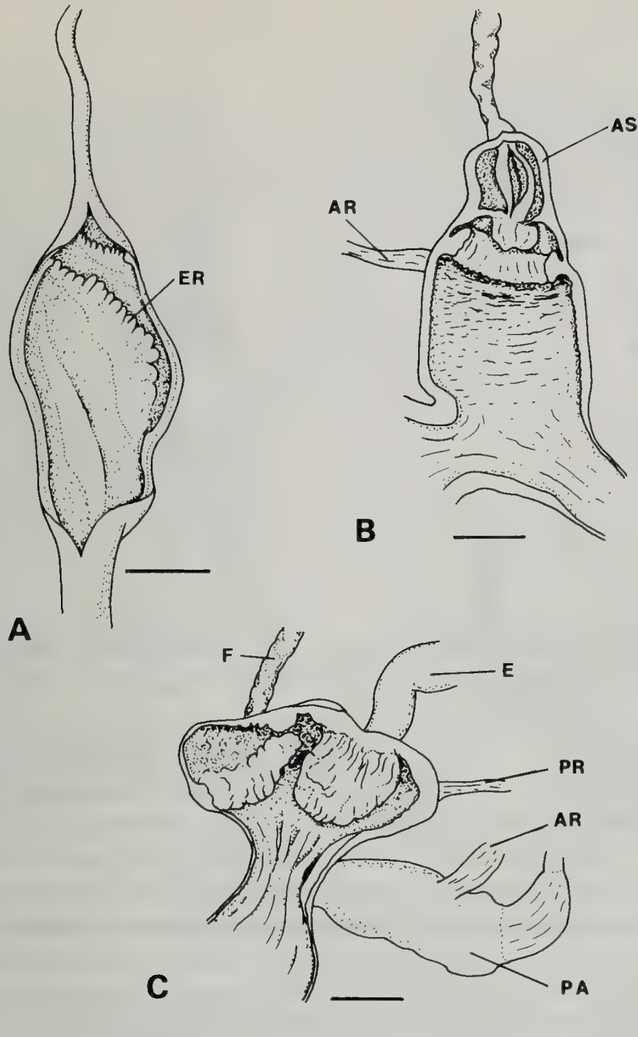

Fig. 16 A. Epiphallus; B. Penial appendix; C. Penis. *Edouardianatalensis*, Pietermaritsberg, South Africa. Scale line 1 mm.

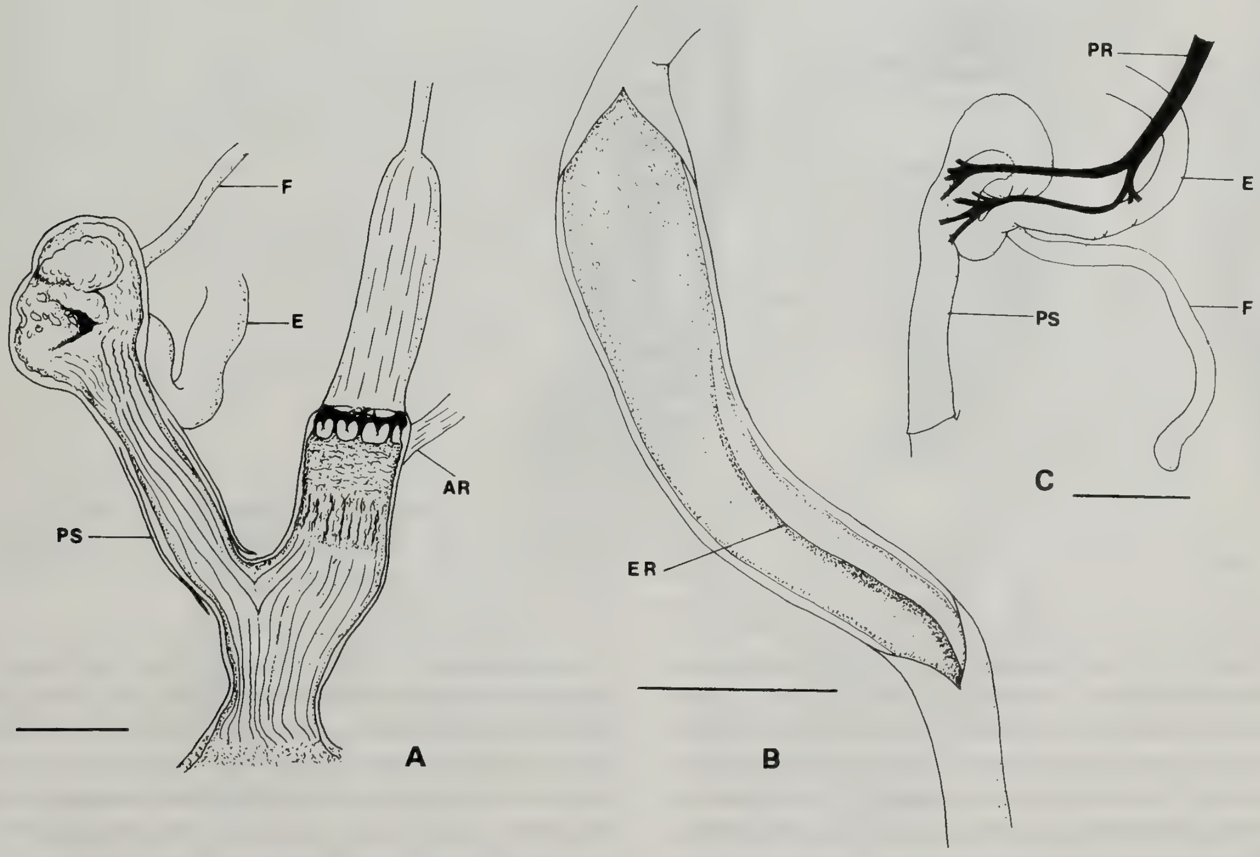

Fig. 17 A. Penis and appendix; B. Epiphallus; C. Penial retractor muscle. *Amimopina macleayi*, Daly River, Australia. Scale line 1 mm.

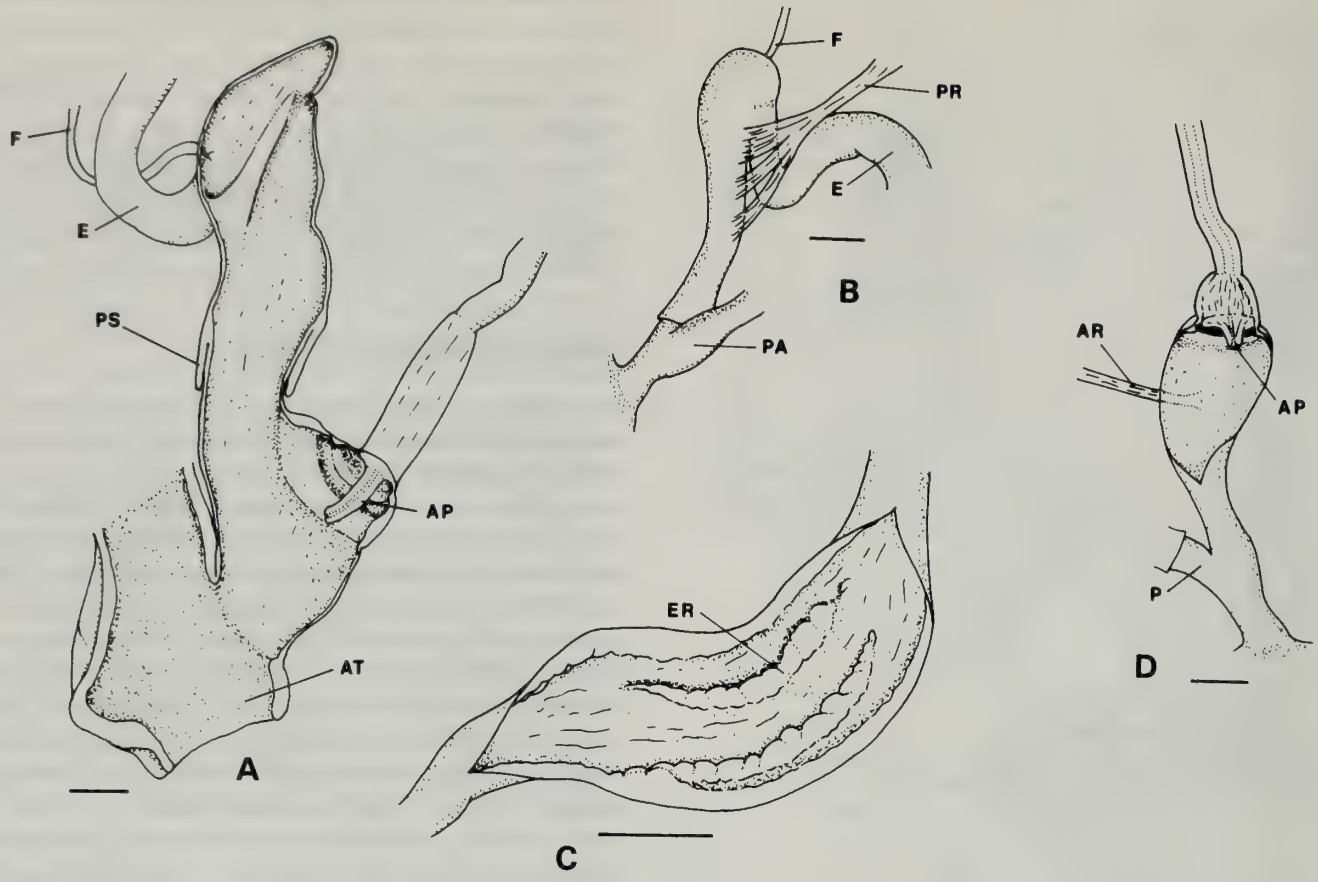

Fig. 18 A. Penis and appendix; *Rhachistia chiradzuluensis*, Thika, Kenya. B. Penis; C. Epiphallus; D. Penial appendix; *Rhachistia histrio*, Maré, Loyalty Islands. Scale lines 0.5 mm.

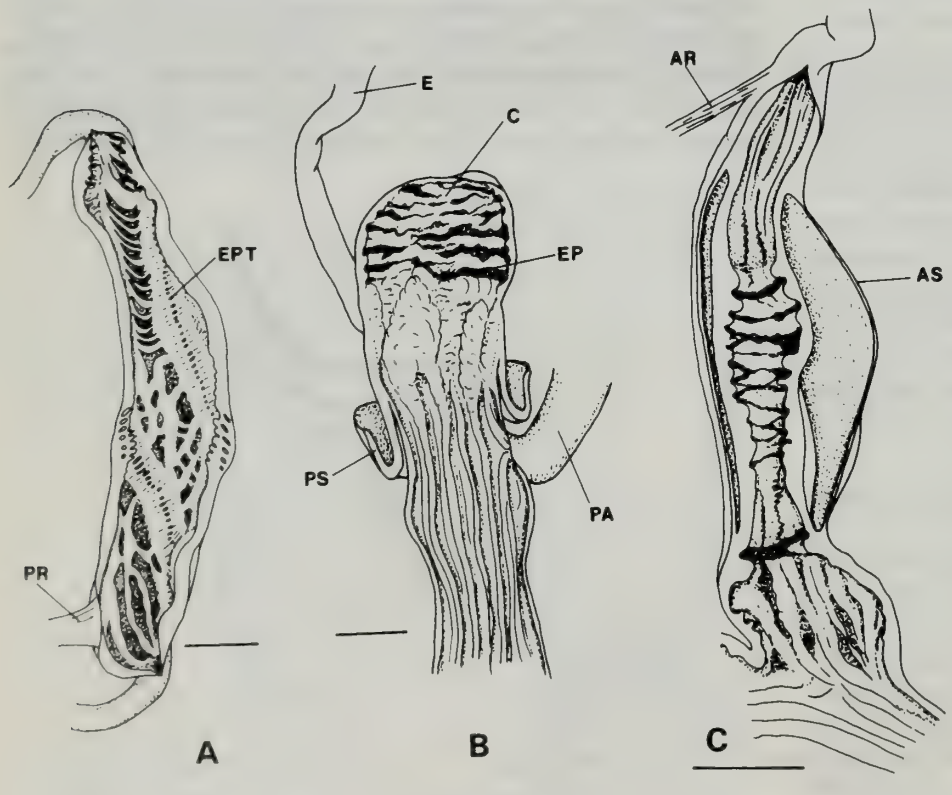

Fig. 19 A. Epiphallus; B. Penis; C. Penial appendix. *Cerastus trapezoidea*, Kitale, Kenya. Scale lines 1 mm.

progressively more divided towards margin. Three genera, *Pachnodus*, *Rhachistia* and *Amimopina*, have broad, blunt mesocones on the central and lateral teeth rather than the more-usual pointed cusps (Character 21), and a distinction is also made between the presence or absence of ectocones on the central tooth (Character 22), the former being the more-usual state. Other radular features, such as the development of raised, sharpened lateral ectocones, appear to be functional correlates of other modifications and so are not treated separately for the cladistic analysis. The prominently developed endocones in *Amimopina* (Solem, 1973) and the various types of modification which have taken place in the marginal teeth of certain genera, would appear as autapomorphies and therefore have been excluded from the analysis; they are, however, considered further in the discussion.

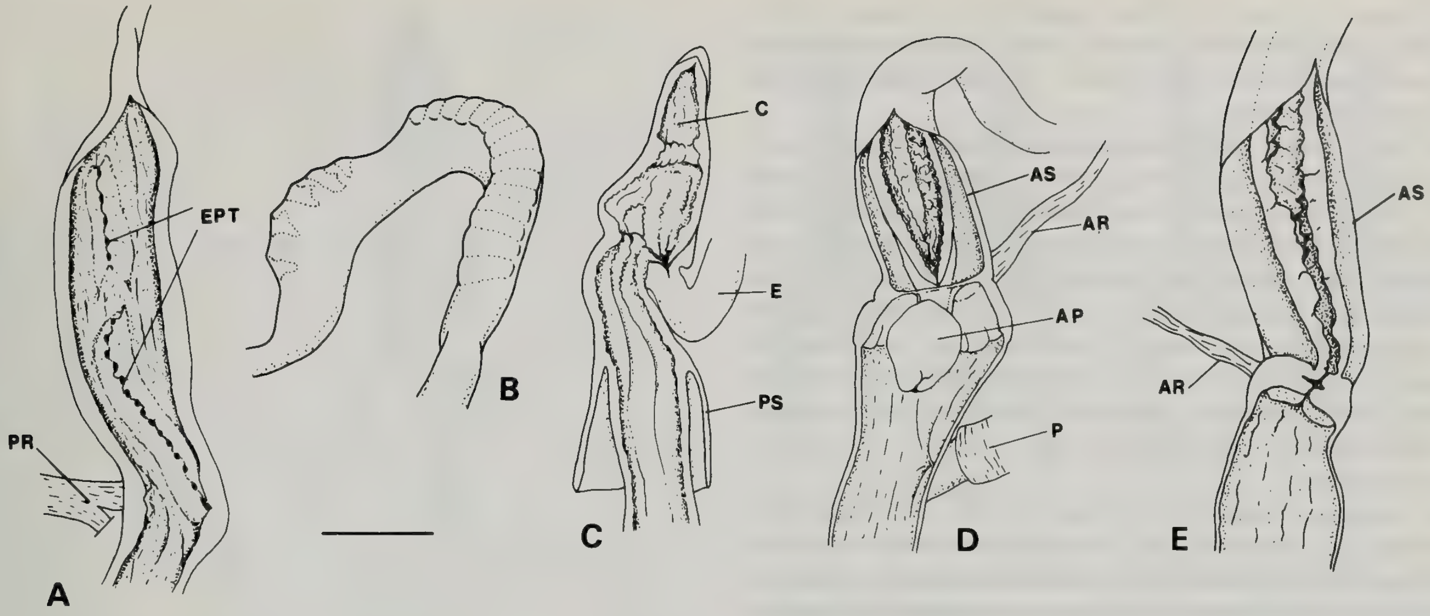

Fig. 20 A, B. Epiphallus; C. Penis; E. Penial appendix. *Conulinus rutshuruensis*, Thika, Kenya. D. Penial appendix. *Conulinus daubenbergeri*, between Marango and Kilimanjaro, Tanzania. Scale line 1 mm.

CLADISTIC ANALYSIS

Table 3 shows the matrix of the twelve taxonomic groups and twenty-two characters used for the cladistic analysis. The taxa represented are all generic units, with the exception of *Edouardia* where small and large species groups have been distinguished following Connolly (1939). Autapomorphic characters have been excluded as recommended by Swofford (1985). Most characters are scored as binary, but five (Characters 1, 2, 9, 10, 20) are represented as ternary. Of these latter characters, only Character 1 has been ordered (see above), the remainder being treated as unordered for the purposes of analysis. No attempt was made to weight the characters. The analysis was undertaken using the PAUP program of Swofford (1985), Version 2.4.1, which is based on the Wagner criterion that the best tree is the shortest or most parsimonious (*ie.* that involving the fewest number of character-state changes or steps). The matrix size was sufficiently small for the branch-and-bound algorithm (based on Hendy & Penny, 1982) to be used. This algorithm purports to obtain all the most parsimonious trees (Swofford, 1985) although Platnick (1987) has shown that this is not always the

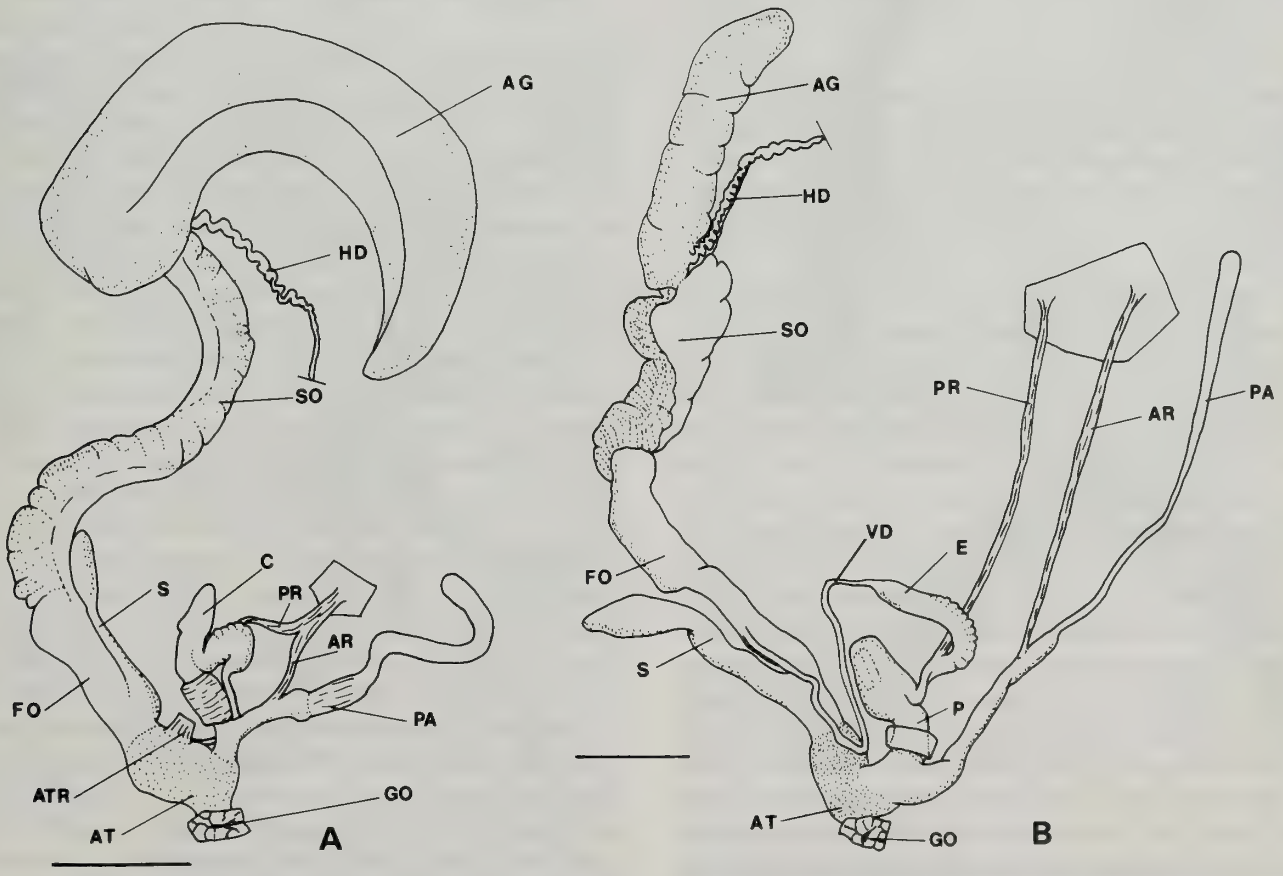

Fig. 21 Genital systems. A. *Rachis punctata*, Dar es Salaam, Tanzania. B. *Achatinelloides sosotrensis*, Socotra. Scale line 2 mm.

case. Following Platnick, all the available optimising options available under PAUP were used, as well as various levels of hold, and the BLRANGE option, but no additional trees were found in this way.

The PAUP run produced three equally parsimonious trees, each with a length of 42 steps and a consistency index of 0.643. Two of these trees are accounted for by an unresolved trichotomy involving the two groups of *Edouardia* with the *Rhachistia* and *Amimopina* pairing; in the third tree this trichotomy was resolved with the two *Edouardia* emerging as sister groups. This problem is perhaps best overcome by treating *Edouardia* as a resolved monophyletic taxon for the purposes of the following discussion, in which the character-state changes involved in this area of the tree are considered in more detail.

The resulting cladogram is shown in Fig. 28. The entire Cerastinae are separated from the designated outgroup (*Ena*) on the basis of six characters of the soft anatomy, three of which may be considered strong synapomorphies defining the subfamily: the presence of renal and rectal folds or ridges (Characters 1, 2) and of a pigmented atrial region (Character 13) are, with very few exceptions, characteristic of the whole group. There are also changes in epiphallar ornamentation (Character 4), with the development of a longitudinal row of spines, and in the insertion of the penial retractor which moves from the penis to the epiphallus (Character 9).

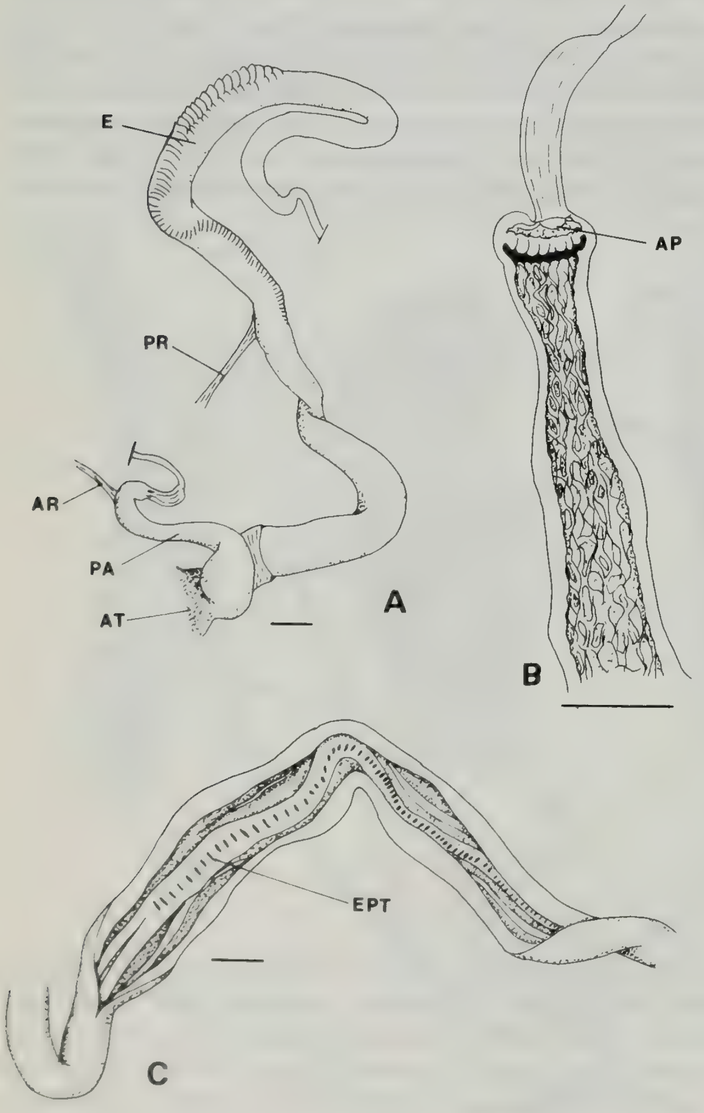

Fig. 22 A. Male terminal genitalia; B. Penial appendix; C. Epiphallus. *Pachnodus silhouettanus*, Shilouette, Seychelles. Scale lines 1 mm.

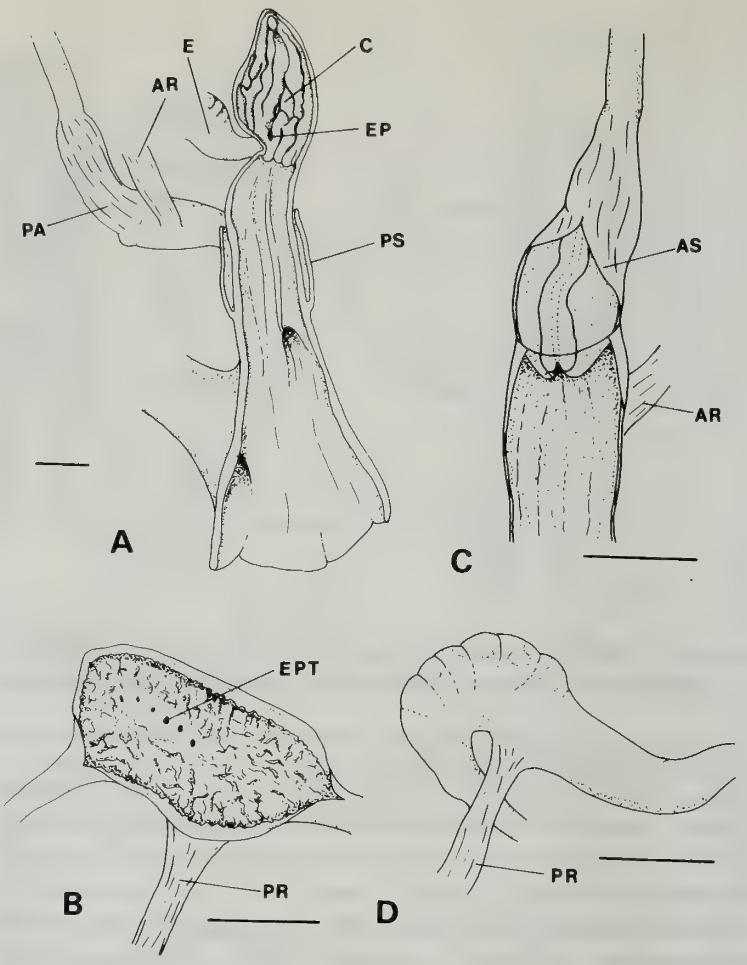

Fig. 23 A. Penis; B. Epiphallus, C. Penial appendix; D. Epiphallus. *Rachis punctata*, Dar es Salaam. Scale lines 0.5 mm.

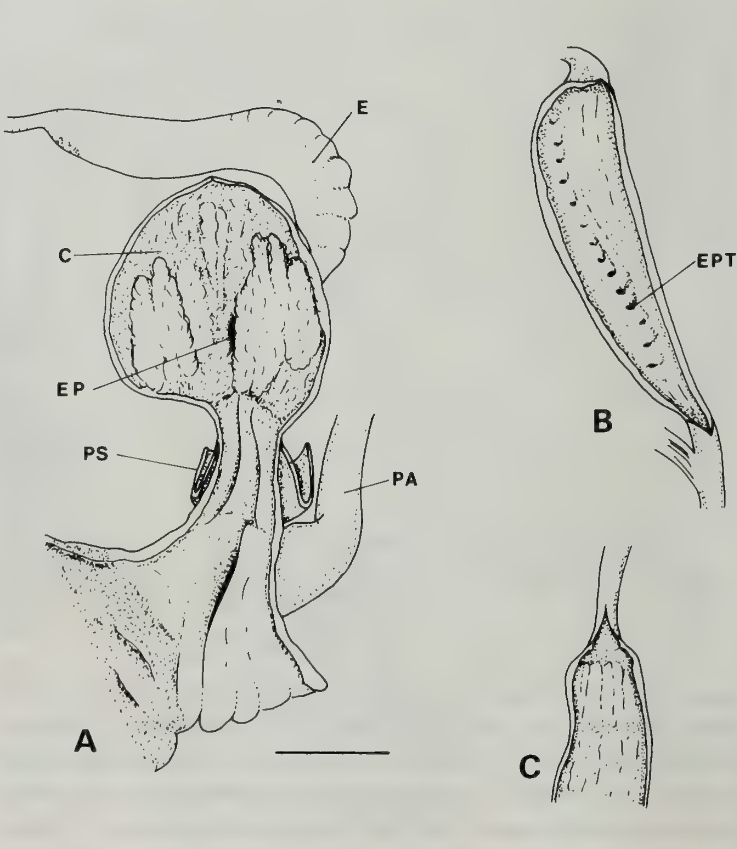

Fig. 24 A. Penis; B. Epiphallus; C. Penial appendix. *Achatinelloides balfouri*, Socotra. Scale line 1 mm.

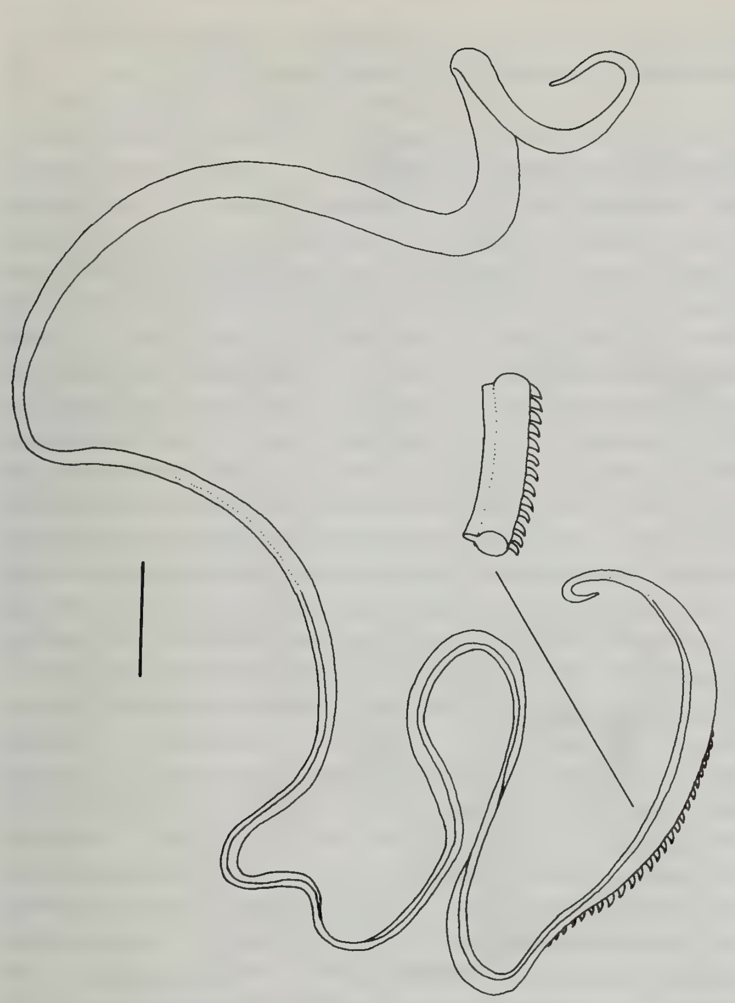

Fig. 25 Spermatophore. *Rhachistia rhodotaenia*, Nairobi-Mombassa Road, Kenya. Scale line 1 mm (for enlargement, 0.5 mm).

Additionally, an open umbilicus to the shell develops at this level of the cladogram (Character 19), which characterises of all but two of the genera.

The most primitive genus in the cladogram is *Pachnodus*, which lacks a penial caecum (Character 10). It does, however, possess a highly modified 'arboreal' radula (Characters 20–22) and a prominent tail crest (Character 14) which it shares with the two succeeding genera *Cerastus* and *Conulinus*. These two genera differ from *Pachnodus* in having a well-developed penial caecum (Character 10) which occurs in one of two basic forms throughout the remainder of the Cerastinae, and in modifications to the penial appendix (Character 6). *Conulinus* lacks the shell lip (Character 17) found in both *Pachnodus* and *Cerastus*. These three genera together form a relatively closely related group of primitive taxa, which can be contrasted with the more-advanced taxa which make up the rest of the cladogram. These remaining genera are separated into two quite distinct clades.

The first of these clades includes *Rachis, Zebrinops, Euryptyxis* and *Achatinelloides* and appears the more primitive, or at least the less differentiated of the two. It shares many features with the preceding genera *Cerastus* and *Conulinus*, notably in the terminal genitalia, but is separated in the tree on the basis of shell pigmentation (Characters 15, 16) and the base of the appendicular stalk which becomes unthickened (Character 5). *Rachis* retains joined penial and appendicular retractor muscles (Character 8) but in the three remaining genera these originate separately on the lower lung wall. *Zebrinops* is distinguished by having its retractor muscle inserted on the central stalk of the penial appendix (Character 7) rather than on its base, whilst *Euryptyxis* and *Achatinelloides* form a terminal sistergroup united on the basis of a secondarily unenclosed base to the appendicular stalk (Character 6) and, uniquely in the cladogram, a well-developed columellar fold and completely closed umbilicus on the shell (Characters 18, 19). *Euryptyxis* shows two reversals in shell characters, losing colour patterning (Character 16) and developing an often very pronounced apertural lip (Character 17).

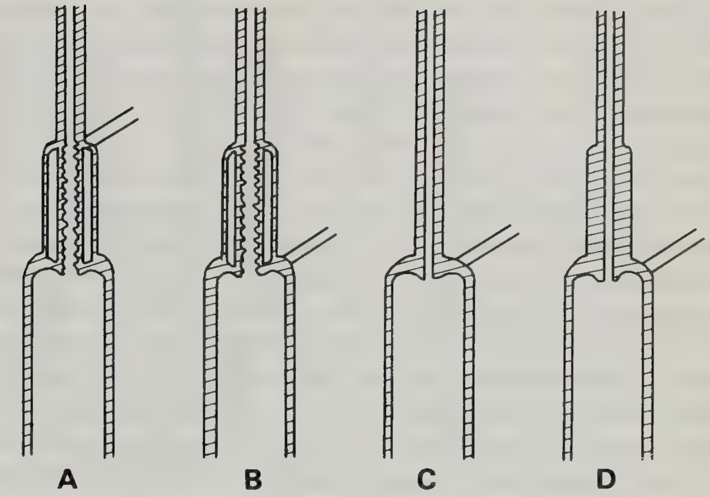

Fig. 26 Diagramatic representation of structural patterns at the junction of the basal and central portions of the cerastine penial appendix.

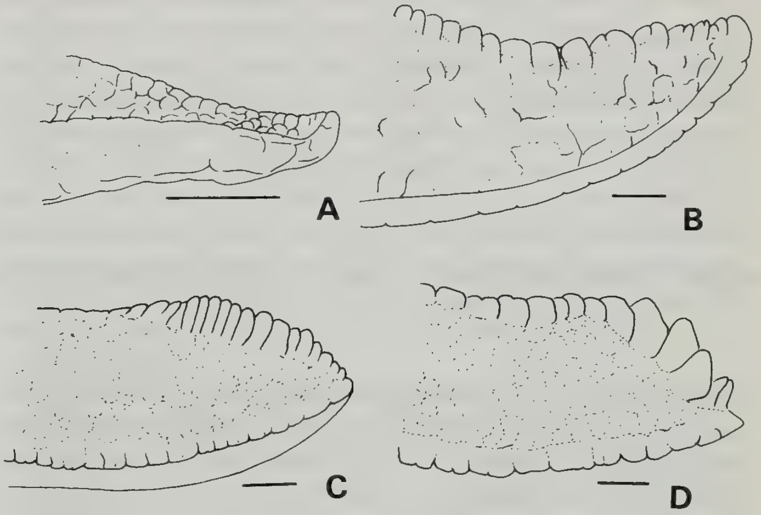

Fig. 27 Tail and tail crest. A. *Edouardia tumida*, Mombassa Island, Kenya; B. *Conulinus rutshuruensis*, Karura Forest, Nairobi, Kenya; C. *Pachnodus silhouettanus*, Silhouette, Seychelles; D. *Cerastus somaliensis*, Daloh Gudun, Somali Republic. Scale line 1 mm.

The second clade comprises the three genera *Edouardia, Amimopina* and *Rhachistia*. These form a strongly differentiated group of closely related taxa, separated in the cladogram by no less than eight character-state changes. Of these, seven can be considered to characterise the clade as a whole. The renal fold fuses to the kidney wall along most of its length to form a ureteric tube (Character 1), the so called 'pseudosigmurethrous' condition (Solem, 1964). All three genera have a reduced spermathecal stalk (Character 3) and secondarily simplified epiphaller ornamentation of longitudinal ridges rather than pits (Character 4), as well as a modified penial

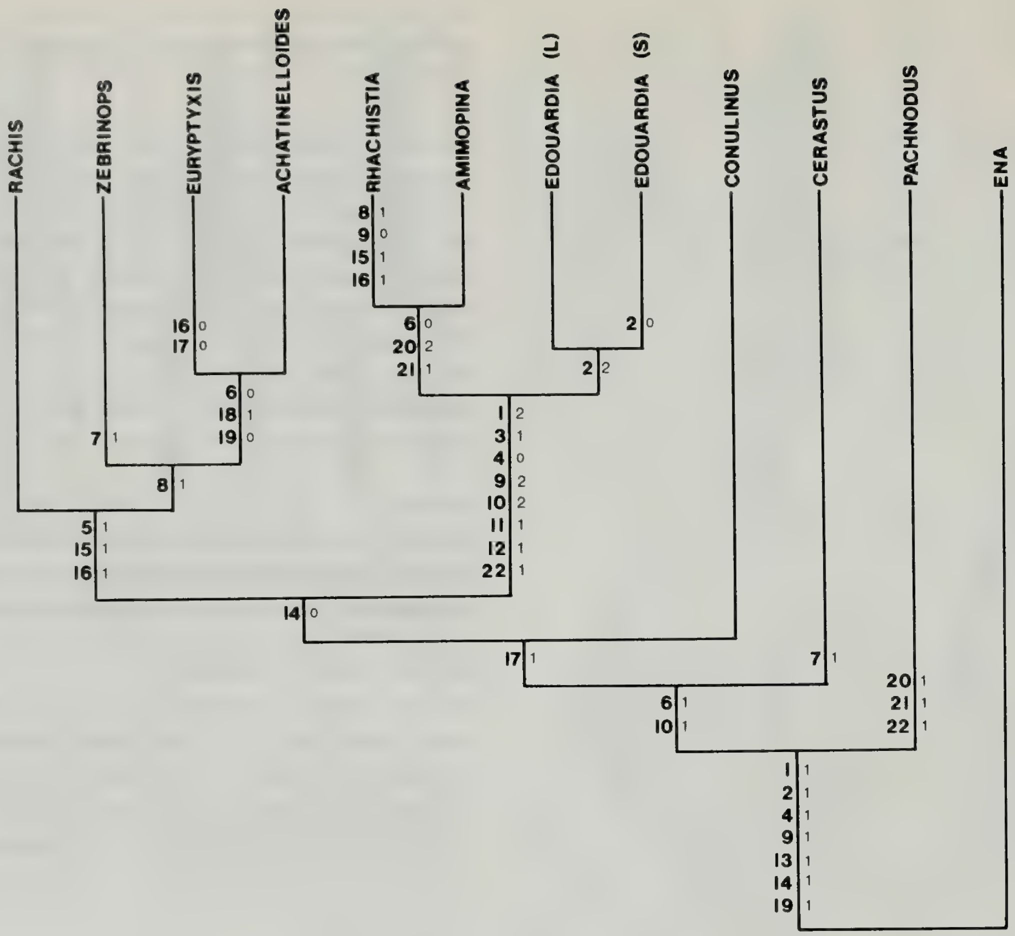

Fig. 28 Cladogram of cerastine genera. Characters are numbered at each node from 1–22 in bold, character states from 0–2 in feint.

caecum bearing a well-developed flagellum (Characters 10, 11, 12). In addition, the ectocones on the central tooth of the radula are lost (Character 22). The small and large groupings of *Edouardia* form part of an unresolved trichotomy in two of the trees, but are resolved in the third where they are paired as a sister group; the former show complete loss of the rectal fold (Character 2), as do many *Rhachistia*, whilst in the large forms the fold is only partially reduced to a thin ridge. Both share with *Amimopina* a double insertion of the penial retractor muscle onto the penis and epiphallus (Character 9) which is subsequently reversed in *Rhachistia*. *Amimopina* retains the complete rectal fold (the plesiomorphic cerastine condition of Character 2), but is united as a sister group with *Rhachistia* in all three trees as both share a simplified base to the appendicular stalk (Character 6) and similar modificiations to the shape of the radular rows, as well as of the individual teeth (Characters 20, 21). *Rhachistia* differs from *Amimopina* in having a pale, patterned shell (Characters 15–16), and also in having a separate origination of the penial and appendicular retractor muscles (Character 8) and a single insertion of this muscle onto the penis (Character 9).

DISCUSSION

The results of the cladistic analysis lend strong support to the hypothesis that the Cerastinae represent a monophyletic taxon in the sense of Hennig (1966), their monophyly being firmly based on a series of independent anatomical characters of the reproductive and excretory systems. Moreover, the cerastines differ from the northern Enidae (the selected outgroup) in a number of additional features, such as the presence of a muscular penial sheath and the absence of a mantle gland and hermaphrodite-duct diverticulae, which did not show variation between genera and therefore were not used in the analysis, but which nevertheless represent taxonomically informative characters. A consideration of the wider significance of reproductive, excretory and shell features in the evolution of the Orthurethra has been given by Nordsieck (1985; 1986).

Two broad groups of taxa can be distinguished in the cladogram: a main lineage of genera possessing open renal and rectal grooves in the pallial cavity, and a second, well-defined clade which branches off above the three basal genera in the cladogram. This second group comprises three genera, *Edouardia, Rhachistia* and *Amimopina*, all of which have a closed, pseudosigmurethous ureteric tube. These various changes to the cerastine excretory system have given rise to a more-complex pallial arrangement than is found in any other orthurethran group, and which perhaps represents the most characteristic feature of the Cerastinae as a whole. Although a few other orthurethran genera such as *Acanthinula* have developed a closed renal ureter (Watson, 1920), the complete rectal fold or ridge of the cerastines which runs the full length of the lung, apparently is unique within the Orthurethra. In life these pallial folds would delimit excretory from respiratory areas within the cavity, and thus presumably increase the efficiency of both systems. The partial or complete closure of the renal fold would appear to be a further adaptation to xerophilic conditions. It is associated with a tendency towards reduction or even complete loss of the rectal fold in some species of *Edouardia* and *Rhachistia*, but the reasons for this are unclear.

The precise adaptive functions of many of the critical reproductive features are similarly obscure. In the female system, the extreme reduction of the spermathecal stalk found in the pseudosigmurethrous group, and the development of the highly characteristic pigmented spongy tissue in the atrium/vagina of all genera are both of uncertain significance, although the latter becomes everted at copulation and may well have a secretory function. The spermatheca is used to store and then break down the spermatophore after copulation, and in many northern enids exceptionally long spermatophores are housed in a special spermathecal diverticulum branching off the main spermathecal stalk. It is therefore surprising that spermathecal stalk reduction in the pseudosigmurethrous cerastines should be associated with the relatively long spermatophores found in this group, and that a spermathecal diverticulum is not known in the Cerastinae.

Some of the most intriguing changes in the reproductive system have taken place in the terminal male genitalia. A muscular penial sheath was found in all dissected cerastine genera, but does not appear to have been recorded in any other orthurethran group. It is presumably associated with evertion of the penis and possibly also ejection of the spermatophore, but its development varies enormously between genera. This sheath (not to be confused with the 'penial sheath' of Nordsieck (1985) which is simply the lower part of the penial tube, or the sheath which encloses the base of the penial appendix in certain cerastine genera) is wanting in northern enids and thus probably represnts a synapomorphy of the Cerastinae.

The only structure in other Orthurethra which in any way resembles the cerastine penial flagellum (which characterises all the pseudosigmurethrous taxa) is the 'flagellum' of *Solatopupa* and *Granaria* (Steenberg, 1925; Gittenberger, 1973), or perhaps the paired weak 'diverticula' in *Acanthinula* (Steenberg, 1917). However, in neither case do these approach the extreme size of the flagellum found in *Edouardia* or *Rhachistia*. Gittenberger (in. litt.) states that the chondrinine flagellum appears to result from the growing together of the penial and epiphallian tube at the point where the loop of the male part of the genitalia typically curves, and considers that this condition is not homologous with that of the Cerastinae. This latter is also reminiscent of the short appendix found in the New Caledonian charopid *Pararhytida*, which was hypothesised to have a secretory function (Mordan & Tillier, 1986). The cerastine flagellum is a fairly simple structure which, unlike the penial appendix, does not appear to be eversible, and this type of organ seems to have been developed independently in a number of stylommatophoran lineages. On the evidence of the reproductive anatomy figured by Zilch (1972; Fig. 5), the west African genus *Altenaia* should be included in the pseudosigmurethrous group as it too has a flagellate penis. *Altenaia* also lacks a pronounced spermathecal stalk, a further characteristic of this clade.

A highly distinctive and elaborate penial appendix is developed in numerous orthurethran groups, and the close structural similarities suggest that this organ, unlike the flagellum, is homologous throughout the suborder. In the Cerastinae it has undergone considerable change in its lower region involving elaboration of the wall of the lumen at the base of the central stalk, as well as enclosure of this area of the stalk by a muscular sheath. These changes are found in *Cerastus* and *Conulinus*, and apparently are retained as a primitive character in *Edouardia* on the one hand, and *Zebrinops* and *Rachis* on the other. The appendicular retractor muscle has also moved upwards onto the top of the sheath in *Cerastus* and, less obviously so, in *Zebrinops*, but this appears to have taken place independently in the two genera. This arrangement would suggest that the tip of the central stalk as well as the basal portion of the appendix protrudes when the appendix is everted; such an interpretation would not only explain the presence of a muscular sheath, but also the internal sculpturing which would serve to increase the surface area of the everted tip. It is noticeable also that the elaboration of the stalk base in *Cerastus* is associated with a very short basal region to the appendix. These changes could perhaps be most readily understood if the appendix had taken over the intromitent function of the penis as it has in, for example, *Sagda* (Goodfriend, 1986), but this does not appear to be the case in the Cerastinae. Block (1968) has observed copulation in *Zebrinops*, where the penial appendix is everted, but not inserted into the partner; rather, it extends under the shell to the region of the mantle collar. Block suggested that it might function as a stimulator and also act to locate the genital orifice. Mordan (pers. obs.) witnessed copulation in the closely related genus *Euryptyxis*, and observed a similar behaviour pattern. In one individual of the mating pair the everted appendix was inserted under the partner's shell, but in the other the tip of the appendix was applied to the skin just behind the genital orifice of the partner, onto which it secreted a milky white fluid. This fluid did not contain sperm, but it is possible that it included some stimulatory secretion similar to that recorded by Chung (1986) from the mucous glands of *Helix*.

From the analysis it would appear that a joined origin of the penial and appendicular retractor muscles represents the plesiomorphic condition within the Cerastinae, only becoming separated in some of the more-advanced genera. This separation has arisen independently on at least two occasions. Some support for the primitiveness of joined retractors in the Orthurethra is given by an ontogenetic study of *Achatinella* in which the retractors start as a single muscle and become progressively more separated as the animal matures (Pilsbry, Cooke & Neal, 1928).

Shell characters were also utilised in the analysis but, not unexpectedly, showed a high level of homoplasy. In general there was a trend towards paler and more-patterned shell colouration in advanced genera of both terminal clades, associated with an arboreal or more-open habitat preference. This relationship between shell pigmentation and habitat has been well documented in other land-snail groups (*eg*. Woodruff, 1978, for *Cerion*). *Euryptyxis* and *Achatinelloides* were united as sister-taxa largely on the basis of two, shared shell characters: a wide but closed umbilicus and a prominent visible columellar fold. These features are also shared with *Passamaella*, a cerastine genus whose anatomy is now known but which, like *Achatinelloides*, is a Socotran endemic, and it is reasonable to assume that these groups are closely related.

One of the main conclusions to be drawn from the cladistic analysis was the closeness of relationship shown between the genera in the pseudosigmurethrous clade, particularly when compared with their high degree of differentiation from other cerastines. Large carinate *Edouardia* from southern Africa were united with the more-widespread, smaller *Edouardia* either as part of an unresolved trichotomy, or as sister groups in the third tree. This last tree was resolved by assuming that the two *Edouardia* groups shared a reduced rectal fold, which is subsequently lost in the smaller species. Such secondary reduction and then loss of the fold is not an unreasonable hypothesis, although the adaptive value of such a change is not obvious.

The genus *Rhachistia* was introduced by Connolly (1925: 163) to include a number of species previously placed in *Rhachidina*. *Rhachistia* was separated by Connolly on shell and radular characters, and in particular by having a radula 'of a specialised arboreal type'. In general the radulae of cerastines are remarkably uniform in appearance, and similar to those of the northern Enidae (Mordan, 1986, fig. 5), but the type species of *Rhachistia, R. rhodotaenia*, does have unusually sharply angled tooth rows and broad, blunt cusps on the centrals and laterals. In this respect it differs markedly from the type species of *Rhachidina, R. tumefacta*, as figured by Thiele (1921; p. 1.4, fig. 2). Of the fourteen species whose radulae were examined and which have been attributed to one or other of these two genera, only *usagarica* Smith from East Africa appears certainly to belong to *Rhachidina*. All the rest have a radula of the *Rhachistia* type. Thiele's figure of *tumefacta* shows that it develops prominent endocones on the lateral teeth, as does *usagarica*, a feature shared only with *Amimopina*. Both *usagarica* and *tumefacta* also have a clearly developed apertural lip on the shell, and this is probably characteristic of the genus. None of the non-African species in the *Rhachistia*/*Rhachidina* complex have this lip, and thus it would seem that *Rhachidina* is a very much more restricted genus than previously believed, perhaps comprising only a small number of exclusively African taxa. However, its precise limits and relationships cannot be resolved until details of the soft anatomy of *tumifacta* are known.

Amimopina is represented as the sistergroup of *Rhachistia*, the relationship being based in part on shared possession of a modified radula of the arboreal type. Although this is represented in the cladogram as a synapomorphy for the group, Solem (1973) has argued from a detailed analysis of scanning electron micrographs that the modifications have originated separately in these two groups, the main differences being in the inter-row support mechanism and the degree of ectoconal development in the lateral teeth. Whilst Solem's contention that the soft anatomy of the two is not similar, and therefore that they are only distantly related within the Enidae, is no longer tenable, it may nevertheless remain that certain radular modifications have been independently derived in the two genera. The 'arboreal' radula of *Pachnodus* clearly has evolved independently, for although it shows certain parallel similarities with that of *Rhachistia*, such as the blunt mesocones and sharp, raised ectocones on the lateral teeth, there are marked differences in row shape and in the form and number of the marginal teeth (van Mol & Coppois, 1980). In particular, the row of marginal teeth of *Pachnodus* is *backwardly* directed, whereas in *Amimopina* and *Rhachistia* the entire lateral and marginal rows are angled *forward* from the central tooth.

The three most primitive genera in the cladogram are *Pachnodus, Conulinus* and *Cerastus*; all are essentially forest/montane taxa, and this would therefore appear to be the most-likely ancestral habit of the Cerastinae. Judged by the present-day habitat preferences of the remaining genera, subsequent evolution should be viewed as a progressive trend towards a xerophilic life style. One feature which may be significant in this context is the caudal crest, which is only present (or at least only prominently developed) in *Pachnodus, Cerastus* and *Conulinus*. Its function is unknown, but it resembles the paired tail crests of some subulinids (Odhner, 1921) and, to a lesser degree, the 'keel' of limacid and milacid slugs. No equivalent structure appears to have been recorded from other Orthurethra. It would seem to represent a primitive feature of the Cerastinae which has been subject to selection for reduction and ultimately loss in the more xerophilic genera, possibly because one of its effects would be to increase the evaporative surface-area of the tail.

Although the general pattern of relationships in the cladogram appears to be fairly robust (for example, the plesiomorphy of *Pachnodus*; the subsequent division into distinct pseudosigmurethrous and non-pseudosigmurethrous clades; and the terminal sister-group relationship of Socotran endemics with Arabian genera), the impression given in other parts of the cladogram is of mosaic evolution and, as a result, a topology which appears rather unstable in that it is based on a small number of often weak characters. This is particularly true of relationships within the pseudosigmurethrous clade, even though the monophyly of this particular clade has been very clearly established.

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APPENDIX 1

List of material dissected

Achatinelloides balfouri. Socotra. Leg. Prof B. Balfour. 2 spec.

Achatinelloides socotrensis (L. Pfeiffer). Bed of River Hanifa, 2 miles Hadibo, Socotra. Leg. Oxford University Socotra Expedition, 11.viii.1956. 3 specs. Reg. No. 1957.7.10.1–3. 3 specs.

Amimopina macleayi (Brazier). Cameron's Bay, Darwin, Northern Territory, Australia. Leg. V. Kessner, l.xi.1981. 2 immature specs.

Amimopina macleayi. Oolloo Crossing, E. bank of Daly River. Northern Territory, Australia. Leg. V. Kessner, 16.iii.1986. FMNH 215272/17. 2 specs.

Amimopina macleayi. N.W. tip Putairta Hill, Kimberley, Western Australia. Leg. A. Solem, L. Price, W. Emberton, 8.vi.1984. FMNH 211955/2. 2 immature specs.

Cerastus trapezoidea (Martens). Kitale, Kenya. Leg. Mrs R. Tweedie. 1 spec.

Cerastus somaliensis (E.A. Smith). Daloh Gudun, Somali Republic. Leg. C.F. Hemming. 2 specs.

Conulinus daubenbergeri (L. Pfeiffer). Rain Forest between Marango and Kilimanjaro, Tanzania, 2200m. Leg. and det. K.L. Pfeiffer. 1 spec.

Conulinus rutshuruensis (Pilsbry). Karura Forest, Nairobi, Kenya. Leg. Polhill, 20.v.1960. 1 spec.

Edouardia sordidula (von Martens). Wazo Hill, nr Dar es Salaam, Tanzania. Leg. P.F. Kasigwa. 1 spec.

Edouardia tumida Taylor. Mombassa Island, Kenya. Leg. B. Verdcourt, ix.1962. 3 specs.

Edouardia natalensis (Pfeiffer). Pietermaritzburg, South Africa. 3 specs.

Edouardia cf. *metula* (von Martens). Bally, Nairobi, Kenya. Leg. B.

Verdcourt. 2 specs.

Pachnodus silhouettanus (van Mol & Coppois). Silhouette, Seychelles. Leg. E.S. Brown, 15.ii.1953. 1 spec.

Rachis punctata (Anton). Dar es Salaam, Tanzania. Leg. W.E. Calton, xi.1956. 3 specs.

Rachis punctata. Sabaki, Nr Malindi, Kenya. Leg. R. Polhill, xi. 1961. 1 spec.

Rhachistia histrio Pfeiffer. Maré, Loyalty Islands. Leg. W.W. Perry. Reg. No. 1875.11.3.1. 2 specs.

Rhachistia chiradzuluensis (E.A. Smith). Chania Gorge, Thika, Kenya. Leg. B. Verdcourt, det B. Verdcourt. 1 spec.

Rhachistia chiradzuluensis. Thika, Kenya. Leg. B. Verdcourt, v. 1960.

Rhachistia aldabrae (von Martens). Aldabra Atoll. Leg. G.Lionnett, det B. Verdcourt.

Rhachistia rhodotaenia (von Martens). Nairobi-Mombassa Road, Kenya. Leg. R. Polhill and B. Verdcourt, 17.iv.1960. 3 specs.

Zebrinops maunoiriana Bourguignat. Erigavo, Somali Republic. Leg. C.F. Hemming. 2 specs.

Zebrinops maunoiriana. 1 mile SE of Shiek, Somali Republic. Leg. C.F. Hemming. 1 spec.

APPENDIX 2

Abbreviations used in figures

A	Anus	HG	Hermaphrodite gland
AG	Albumen gland	K	Kidney
AP	Appendicular papilla/pore	MC	Mantle collar
AR	Appendicular retractor muscle	P	Penis
		PA	Penial appendix
AS	Appendicular sheath	PN	Pneumostome
AT	Atrium	PR	Penial retractor muscle
AU	Auricle	PS	Penial sheath
C	Caecum	RNF	Renal fold
E	Epiphallus	RNU	Renal ureter
EPT	Epiphallar pit	RT	Rectum
ER	Epiphallar ridge	RTF	Rectal fold
F	Flagellum	S	Spermatheca
FO	Free oviduct	SO	Spermoviduct
GO	Genital orifice	PV	Pulmonary vein
HD	Hermaphrodite duct	VE	Ventricle

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A redescription of the uniquely polychromatic African cichlid fish *Tilapia guinasana* Trewavas, 1936

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Synopsis. *Tilapia guinasana*, endemic to a single sink hole (surface area *ca.* 2800 m^2) in northern Namibia, is unique amongst the species of that genus because of its extensive polychromatism, a phenomenon not recognised when the species was first described from preserved material (Trewavas, 1936). Five principal and non-sexlimited colour forms (one with several variants) are now known from this single population.

Questions have been raised about the specific status of *Tilapia guinasana*, with suggestions ranging from it being an aberrant population of the widespread *Tilapia sparrmanii* to the possibility that the different morphs represent distinct species. Recent fieldwork, and the additional material now available for detailed study, all indicate that *Tilapia guinasana* is indeed a distinct and polychromatic species with several unique morphological and anatomical features, especially osteological ones. These features are discussed and consideration is given to possible environmental influences on their phenotypic expression.

The phylogenetic relationships of the taxon remain uncertain pending a fully cladistic analysis of the genus *Tilapia*, but the derived status of the species within at least part of the genus can be established.

INTRODUCTION

Tilapia guinasana is endemic to a single sink-hole, Lake Guinas, situated in the northern part of Namibia (17°20′E, 19°19′S). Since Lake Guinas has a surface area of only *ca.* 2800 m^2, *T. guinasana* has the smallest area of endemicity of any known *Tilapia* species.

At the time of its discovery by Jordan in 1931, *T. guinasana* seemed not to be present in the nearby Lake Otjikoto (17°30′E, 19°10′S; surface area *ca.* 4200 m^2), since collections from that lake yielded only the haplochromine cichlid *Pseudocrenilabrus philander dispersus* (Trewavas). However, there are records that, in 1922, the species was introduced into Lake Otjikoto (A.J. Ribbink, pers comm., based on a letter from Mrs T. Schatz of the Tsumeb Museum) where it is now established (together with another translocated tilapiine species, *Oreochromis mossambicus* [Peters]; see also Skelton, 1990).

The species displays a degree of colour polymorphism unique amongst tilapiine fishes, and is the only polychromatic member of its genus. That phenomenon alone makes *T. guinasana* of particular interest to both cichlid taxonomists and to evolutionary biologists, an interest enhanced by the species' limited distribution, its physical and therefore genetical isolation, its small population size, and its departure in several osteological features from its supposed nearest relative, the widely distributed *Tilapia sparrmanii* Smith.

The additional morphological, anatomical and ethological information now available, together with the well-preserved and annotated material at hand, permit a more detailed description of the species than was possible before, as well as a reconsideration of its intrageneric relationships, particularly its supposed close affinities with *T. sparrmanii* (see Trewavas, 1936) and its suggested derivation from an isolated population of that species (Penrith, 1978).

Polychromatism in *Tilapia guinasana*

In her original description of *T. guinasana*, based only on preserved specimens, Trewavas (1936) recorded the coloration as 'Uniformly blackish or particoloured; or, occasionally, with faint traces of a black band from operculum to caudal and another on upper lateral line'. Later visitors to Lake Guinas (Penrith, 1978; Skelton, 1988, 1989), however, reported the existence of several distinctive colour forms. Some of these are represented amongst Trewavas' particoloured individuals, the appearance of which matches that of recently preserved specimens whose live coloration is known (personal observations based on field-data provided by A.J. Ribbink).

The existence of such extensive polychromatism in a substratum spawning African cichlid genus otherwise characterized by '. . . no or minimal sexual dimorphism or dichromatism' (Trewavas, 1983: 13), and in which no examples of polychromatism have been reported, aroused the interest of Dr A.J. Ribbink. He, together with several co-workers, twice visited Lake Guinas and made detailed observations on the species (see Ribbink, Greenwood, Ribbink, Twentyman-Jones and van Zyl, 1991).

Although when viewed through the water surface the fishes appear to be either black or light blue, underwater observations revealed the presence of five principal and non-sexlimited colour forms among adult fishes, namely dark blue, olive, olive striped, blue striped, and light blue, the latter category with elements of white, light blue, yellow, and even black blotches in some individuals (Ribbink *et al.*, 1991).

Almost all juveniles less than *ca.* 25 mm standard length are greyish-green in colour, with seven or eight vertical bars and two longitudinal bands on the body. Occasionally some completely pale blue, almost white, unbarred and unbanded individuals were observed (Ribbink *et al.*, 1991).

In addition, the Ribbink party recorded, on their first visit (April, ie. autumn, 1988), a sixth and numerically smaller colour group which they named 'large black'. All members of this category were noticeably larger (*ca.* 127–150 mm S.L.) than those of other categories, and none was part of any breeding group observed at that time. All other colour forms were, however, represented amongst the breeding pairs (Ribbink *et al.*, 1991). On their second visit to the lake (October, ie. spring, 1989) no 'large blacks' were seen, but individuals of a comparable size (ie. over 120 mm S.L.), and showing three chromatic forms (dark blue, light blue and olive) were observed and seen to be members of the breeding population. Again, there appeared to be a distinct size-gap between these large fishes and other members of their respective colour morphs.

The absence of small black fishes (as seen underwater), and the apparent size-gap existing between individuals of all other colour forms and the 'large black' fishes, as well as the size-gap between the large olive, light blue and dark blue fishes and their co-morphs are phenomena that require further field and laboratory studies. There is no ethological or morphological evidence to suggest that the large specimens are members of a distinct species.

Likewise, there is no morphological evidence to suggest, as might be thought *a priori*, that the various colour morphs are distinct species. That idea is also negated by Ribbink *et al.*'s (1991) underwater observations on the pairing of different colour forms during mating. Those observations indicate that, although some morphs do show a degree of assortative mating (ie. like with like), this is by no means absolute and the level of inter-chromatic matings is such that the morphs of *T. guinasana* must be considered members of a single species.

METHODS AND MATERIALS

The system of external counts and measurements follows that of Trewavas (1983). Gill-raker counts are taken from the outer row of rakers on the first ceratobranchial, and exclude the single raker at the junction of that bone with its epibranchial.

The length of the keel on the lower pharyngeal bone is measured, on the bone's occlusal surface, from the anterior tip of the keel to a horizontal drawn through the point where the lateral margins of the dentigerous surface join the keel (usually at or near the first tooth or teeth of the median tooth rows). The breadth of the bone's dentigerous surface is measured, posteriorly, as the direct distance between the most lateral points of the toothed area on each half of the bone. The length of the dentigerous surface is the greatest distance of the toothed area measured directly from its posterior to its anterior points.

Neurocranial length (Nc.1) is measured directly, along the base of the skull, from the anterior point of the vomer to the posterior point on the condylar surface of the basioccipital.

Material

An asterisk indicates that skeletal preparations are available. Institutional abbreviations are, BMNH: British Museum (Nat.Hist.), RUSI: J.L.B. Smith Institute of Ichthyology, Grahamstown.

Tilapia guinasana (*ex.* Lake Guinas)
Lectotype: BMNH 1935.3.20:32
Paralectotypes: BMNH 1935.3.20: 33–51,* and 1935.3.20: 197–208
Other material from the original collection: BMNH 1935.3.20: 209–233* (see p. 24)
RUSI material collected by Ribbink *et al.*, 1988 and 1989

RUSI 35859 (large black)
RUSI 35860 (large black)*
RUSI 35861 (large olive)
RUSI 35862 (large light blue)
RUSI 35863 (olive)*
RUSI 35864 (dark blue)*
RUSI 35865 (light blue)*

RUSI 35866 laboratory reared; (Light blue; 60 mm S.L.)*
RUSI 35867 laboratory reared; (Olive; 65 mm S.L.)*
RUSI 35868 laboratory reared; (White and blue; 45 mm S.L)*
RUSI 35869 laboratory reared; (Olive, 50 mm S.L.)*
RUSI 35870 laboratory reared; (Olive,* and light blue)
RUSI 35871 laboratory reared; (white and blue,* and light blue)

RUSI material *ex* lake Otjikoto: RUSI 35485*

Tilapia species from southern Africa
T. sparrmanii: RUSI 30342 Okavango delta, Botswana*
RUSI 24197 Okavango delta, Botswana*
RUSI 19265 Lake Bangasi, St Lucia, KwaZulu*
RUSI 24223 Kwando river, Caprivi strip, Namibia*
RUSI 2260 Limpopo system, Transvaal, RSA
RUSI 27923 Mkuze, Yengweni Pan, KwaZulu
BMNH 1907.3.15: 44, Groot Olifants river, Transvaal, RSA.*

T. ruweti: RUSI 23616 Lake Ngami, Botswana
RUSI 30343 Okavango delta, Botswana*
RUSI 30126 Okavango delta, Botswana

T. rendalli: RUSI 23951 Okavango delta
RUSI 26579 Nkomati river
RUSI 27988 Sabi river, Skukuza, northern Transvaal, RSA*
RUSI unregistered. Crocodile river, eastern Transvaal RSA*
RUSI unregistered. Fish pond, J.L.B. Smith Institute (provenance unknown)*
RUSI unregistered. Okavango delta, Botswana*

Tilapia species from elsewhere in Africa:
T. brevimanus: BMNH 1912.4.1: 153*
T. buttikoferi: BMNH 1912.4.1: 163*
T. busumana: BMNH 1902.4.24: 41*
T. cabrae: BMNH 1911.6.1: 154*
T. guineensis: BMNH 1899.11.20: 4*
T. kottae: BMNH 1973.5.14: 1130–1133*
T. mariae: BMNH 1901.8.21: 38*
BMNH 1985.11.12: 199–211*
T. tholloni: BMNH 1981.12.1: 1–12*
T. zillii: BMNH 1907.12.2: 3767*
BMNH 1968.12.13: 30–42*

Oreochromis species:
O. alcalicus alcalicus: BMNH 1966.12.9: 44–86*
O. a. grahami: BMNH 1982.4.22: 32–35*
O. amphimelas: BMNH 1967.8.17: 5–17*
O. mossambicus: RUSI unregistered alizarin preparations of laboratory raised juveniles

All radiographs used in this study are in the J.L.B. Smith Institute except that of *T. guinasana* lectotype, which is in the BMNH collection.

A REDESCRIPTION

Tilapia guinasana

Fig. 1

SYNONYMY. *Tilapia guinasana* Trewavas, 1936. *Novitates Zoologicae 40*: 72–73 (original description).

Tilapia (Trewavasia) guinasana; Thys van den Audenaerde, 1968. *Documentation Zoologique, Musee Royal de l'Afrique Centrale* no. 14: xxvii–xxviii (definition of a new and monotypic subgenus, and designation of *T. guinasana* as type species).

No holotype was designated in the original description of

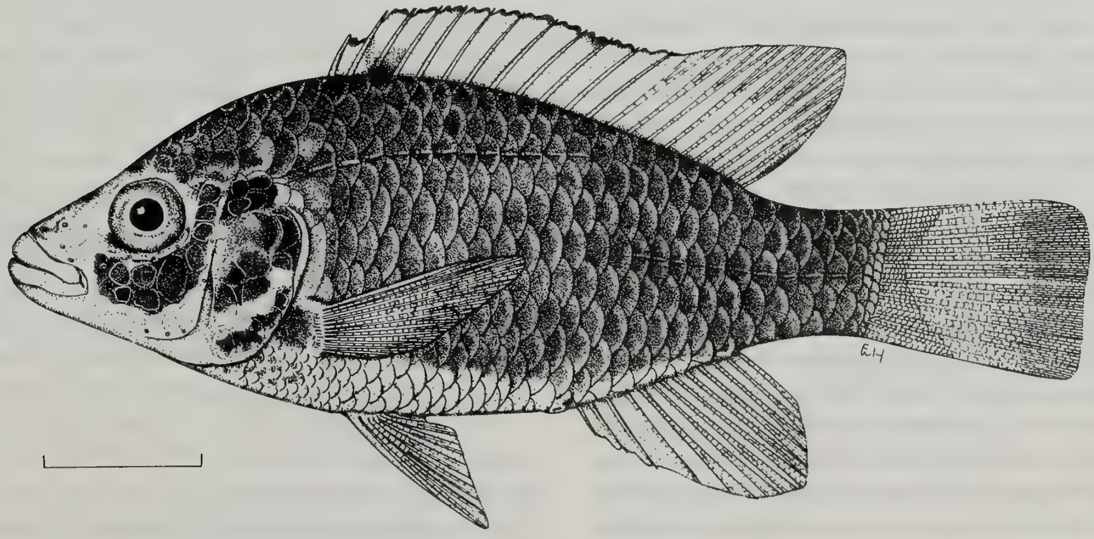

Fig. 1. *Tilapia guinasana*. Specimen from RUSI lot 35865; in life a light blue morph. Scale: 1 cm. Drawn by Elaine Heemstra.

the species. That description, according to Trewavas (1936) was based on 32 specimens, 60–137 mm total length, with specimens '. . . of less than 85 mm included for numerical characters only'; she did, however, note that smaller individuals have a relatively larger eye diameter and fewer teeth but 'Otherwise they agree with older fishes'. The number of smaller fishes examined was not given.

A problem arose when I examined the supposed syntypical series in order to select a lectotype. The single jar housing these specimens contains 56 and not 32 specimens as indicated by Trewavas. The problem is further compounded by the museum register number (repeated on the bottle's label) which covers only 20 specimens, namely 1935.3.20: 32–51.

It is impossible to identify, some 55 years later, the 32 specimens on which Trewavas based her description and thus to separate from the 56 specimens those which are truly syntypical and from which, legitimately, the lectotype may be selected. The largest specimen (137 mm total length) and the smallest (60 mm T.L) studied by Trewavas are readily identifiable, but neither is in a good state of preservation and for that reason I would hesitate to select either as the lectotype. Fortunately another specimen (104.0 mm standard length, *ca.* 126 mm total length) has, under its operculum, a label in Dr Trewavas' handwriting, bearing the legend 'Holotype'. On the assumption that Trewavas examined this specimen and intended to designate it as the holotype, I have chosen it to be the lectotype and assigned to it the British Museum (Nat. Hist.) register number 1935.3.20:32.

That action does not resolve the problem of identifying the 31 other specimens (ie. paralectotypes) on which the original description was based, except of course for the smallest and largest fishes. Since there is no guidance in the International Code of Zoological Nomenclature for settling this conundrum, I have selected, together with the largest and smallest specimens, 29 others to constitute the remainder of the type series. These now carry the BMNH register numbers 1935.3.20: 33–51, and 1935.3.20: 197–208 (the latter numbers still being available on the register page for 20th March 1935). My choice of these particular specimens was based on their relatively better state of preservation than that of the others, their representing as wide a range as possible of preserved colorations, and their coverage of the size range of specimens examined in detail by Trewavas.

Presumably the remaining 24 specimens can no longer be considered part of the type series; they now bear the BMNH register numbers 1935.3.20: 209–233.

The lectotype is a fish of indeterminable sex, 104.0 mm standard length and *ca.* 126 mm total length (the caudal fin margin is damaged), collected by Dr Karl Jordan from Lake Guinas, Namibia. Its preserved coloration, in ethyl alcohol (presumably after formalin fixation) is dark brown, slightly lighter ventrally, with darker brown centres to the flank scales.

In the absence of a phylogenetically based revision of the genus *Tilapia* (*sensu* Trewavas, 1983), it is difficult to comment on Thys' proposed subgeneric categorization of *T. guinasana*. Thys defines the subgenus (within his definition of *Tilapia* which is more inclusive than Trewavas') on the basis of it having 12 (rather than 16) scale rows around the caudal peduncle, and on its strongly granulate scales. Thys places *Trewavasia* between the nominate subgenus (comprising *Tilapia sparrmanii* and *T. ruweti*) and the other two subgenera of his 'Section one' subdivision of the taxon (Thys, 1968: xxvii–xxiv). On the grounds of its polychromatism (a feature not known to Thys), *T. guinasana* certainly would seem to be a distinct lineage within the non-mouthbrooding tilapiines. Its larger and strongly granulate (ie. rugose) scales may, however, be an ecophenotypic response to the water chemistry of the lake (see p. 35).

DESCRIPTION. The meristic and morphometric data used in this redescription of *T. guinasana* are derived mainly from the lectotype and twenty-one other specimens 49.0–151.0 mm standard length (the majority, 15 specimens, being in the size range 50–80 mm S.L.) collected by the Ribbink team in September 1989 (RUSI: 35859–35865). These fishes, rather than the paralectotypes, were used for morphometric and meristic studies because all are in a far better state of preservation, their live coloration is known, and they cover a wider size-range than does the type series. Information on tooth morphology and dental patterns (both oral and pharyngeal) and that on cheek squamation was supplemented by counts and observations made on the paralectotypes.

Trewavas' (1936) morphometric ratios, and her meristic counts, do not depart from those obtained from the new material, and an examination of dental features (oral and pharyngeal) shows few differences between the two samples, except, to a small degree, in some features of the larger specimens now available. Unfortunately it is impossible to associate accurately the preserved colours of the type series with what is now known of coloration in living fishes and in the recently collected specimens which were segregated on the basis of their live colours before fixation. However, no outstanding differences were observed in the preserved colours shown by the two samples collected some 54 years apart.

The small sample of 'large blacks' and large specimens of light blue and olive fishes (totalling 4 specimens) is treated together with the others since in all but two morphometric features (eye diameter and cheek depth) they fall within the ranges determined for the smaller specimens. These proportional differences are explicable on the basis of allometric growth, but the figures for the two characters in the large specimens are given separately (in square brackets) and are not included in the means given for those features in the smaller specimens.

Regrettably from the taxonomic view point, but understandably and commendably from that of conservation, there are restrictions on the number of specimens which may be removed from Lake Guinas, hence the relatively small sample on which this redescription is based.

Depth of body 36.0–46.4 (mean, M, 40.8)% of standard length, with a slight tendency for large fishes to be the deepest; head length 30.8–37.1 (M = 33.4)%. Dorsal head profile in fishes <130 mm S.L. straight (sometimes with a slight concavity above the orbit) from a point above or almost above a vertical through the posterior margin of the preoperculum, and sloping at an angle of 40°–45° to the horizontal. This slope increases to about 50° in the four large fishes (139–151 mm S.L.), where the dorsal head-profile is more concave than in smaller individuals, a consequence of the anteroventral tip of the snout becoming slightly upturned.

Preorbital depth 15.5–23.1 (M = 20.1)% of head length; least interorbital width 29.7–36.4 (M = 34.8)%. Snout slightly broader than long (1.1–1.2 times), rarely as long as broad; its length 31.0–39.1 (M = 35.3)% of head length.

Eye diameter showing slight negative allometry with standard length, 25.4–32.4 (M = 28.7)% of head [20.4–25.5, M = 22.3% in the four largest fishes]. Cheek depth showing positive allometry with standard length, 16.2–23.9 (M = 19.9)% of head length [24.5–28.3, M = 25.8% in the four largest fishes].

Lower jaw 33.3–39.1 (M = 35.2)% of head length, and from as long as it is broad to 1.3 times longer than broad (modal range 1.1–1.2 times longer). Mouth sloping slightly upwards; lips moderately thickened. Maxilla with a variable posterior extent, closely approaching a vertical through the anterior orbital margin in one specimen, but in the others reaching either a point midway between the nostril and the orbit or slightly beyond that point.

Caudal peduncle length 13.0–17.2 (M = 15.2)% of standard length, its length-depth relationships variable, the majority of specimens with the peduncle deeper than it is long (its length 80–90% of its depth) the others with the peduncle slightly longer than deep (1.1–1.2 times). No correlation was found between this ratio and specimen size or coloration.

GILL-RAKERS. 8–11 (rare), mode 10, in the outer row on the ceratobranchial of the first arch. The rakers are short and stout (the anterior one or two shorter than the succeeding ones) and have a characteristic pyramidal shape (Fig. 2) quite unlike the narrow-based, flattened, triangular and more elongate rakers in *T. sparrmanii*. Microbranchiospines are present on the outer faces of gill-arches 2 to 4.

SCALES. On all parts of the body the scales are cycloid and have a very characteristic rugose appearance over their entire exposed surfaces, but especially over the central region in scales on the cheeks and flanks. When compared with the scales of *T. sparrmanii*, those of *T. guinasana* are thicker and denser.

There are 25(f5), 26(f12), 27(f4) or 28(f1), mode 26, scales in the lateral series. In one specimen no scales in the upper lateral-line are pored, but in the others 11(f1), 12(f2), 13(f3), 14(f4), 15(f5), 16(f5) or 17(f1) pored scales are present; pored scales in the lower lateral-line number 7(f2), 8(f7), 9(f7), 10(f5), or 11(f1).

The lowest row of cheek scales is often deeply embedded in a thick layer of skin and thus is invisible unless the skin is removed. This 'hidden' row probably accounts for the greater incidence of two scale rows in the new material than apparently was the case in the specimens examined by Trewavas (1936). Without dissection, many more fishes would appear to have only a single row, (as indeed some do) and thus the difference in the number of cheek scale rows between *Tilapia sparrmanii* and *T. guinasana* noted by Trewavas is artificially exaggerated. Whenever a lower row is present, its scales are much smaller than those in the upper row and are thinner and less rugose.

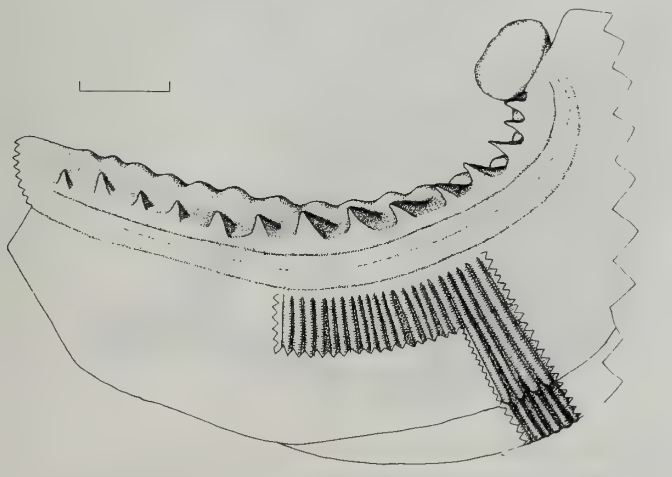

Fig. 2. *Tilapia guinasana*. Outer row gill-rakers on the first gill-arch. Specimen from RUSI lot 35865. Drawn by Elaine Heemstra.

The frequency of cheek scale rows for the 'type' material, at least part of which Trewavas examined, is: 1 row (f3), 2 rows (f45), plus 6 specimens with a single row on one side and two on the other. For the new material, the frequencies for the different conditions are, respectively, 2, 15 and 4. Thus, for the two samples, the model condition is 2 rows, with a single row occurring less frequently than the laterally asymmetrical situation of a single and a double row.

There are 12 scales (13 in one fish) around the caudal peduncle.

The slight size transition between the scales on the chest and those ventrolaterally on the flanks and belly is a gradual one. Except apically, the median scales on the chest are as large as those immediately lateral to them; the apical scales are noticeably smaller.

FINS. The dorsal has a total of 22(f1), 23(f10) or 24(f10) rays (21 specimens only are included here as one fish has an irregular, overlapping junction between the spinous and soft parts of the fin, suggesting some teratological condition), comprising 11(f1), 12(f6), 13(f12) or 14(f2) spinous and 10(f6) or 11 (f15) branched elements. The anal fin has three spines and 7(f1), 8(f4), 9(f13) or 10(f4) rays.

The tips of the longest pectoral rays reach or almost reach a vertical through the anus; the pectoral fin length ranges from 25.3–29.2 (M = 26.8)% of standard length and 74.5–87.5 (M = 80.0)% of head length, neither ratio showing any allometric relationship with standard length.

The longest ray of the pelvic fin extends posteriorly to a little before the anus or to a position between that point and the first anal fin spine. Apparently there is no correlation between the relative length of this fin and the fish's sex or state of sexual activity.

Posteriorly, the margin of the caudal fin varies from truncate to almost rounded, but is truncate or subtruncate in the majority of specimens. The fin is scaled proximally in a roughly crescentic pattern, the horns of the crescent extending to a point about one quarter to one third of the way along the fin's upper and lower margins.

ORAL TEETH. In both jaws most outer teeth are bicuspid. Some unicuspids occur posteriorly, their number on the premaxilla ranging from two or three to as many as fourteen; in the dentary usually only about six such teeth are present. There is no obvious correlation between the number of premaxillary unicuspids and the fish's size, although the lower counts were found in smaller individuals.

Bicuspid teeth (Fig. 3) have a slender body (about half the height of the tooth) which gradually expands into a broader, flattened, and very unequally bicuspid crown. The minor cusp is somewhat obliquely pointed, the major one obliquely truncated and a little protracted, a crown form commonly found amongst *Tilapia* species.

Like the bicuspids, the unicuspids have a relatively compressed crown, but one which is not noticeably wider than the cylindrical body; the tip, at least in unworn teeth, is acutely pointed.

Both bi- and unicuspid teeth are curved adorally from a

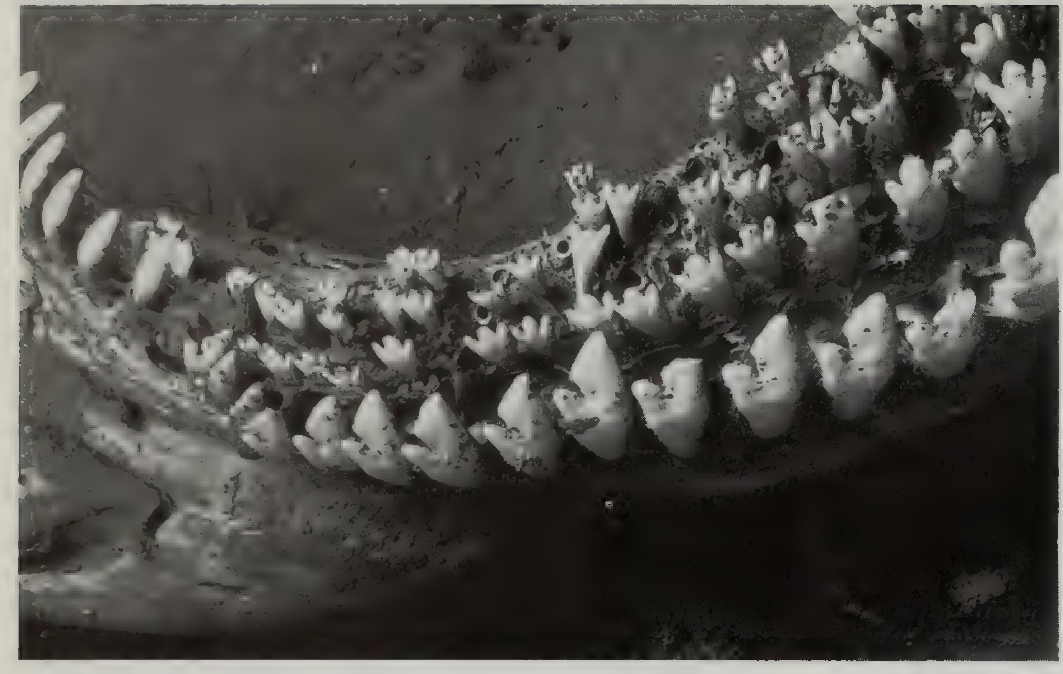

Fig. 3. *Tilapia guinasana*. Oral dentition in part (see also Fig. 9). Anterior and anterolateral region of the right dentary, viewed obliquely from above. The bullate ventrolateral region of the dentary (see p. 30) is clearly visible. Specimen RUSI 35865 (dark blue), 76.0 mm S.L. Magnification × 26.

point about midway along their height. Bicuspids situated anteriorly on the dentary have the most pronounced curvature, in that way ensuring, because of their low implantation on the jaw, that the crowns are almost vertically aligned when the mouth is closed.

Posteriorly, the outer row of teeth on each side of the dentary has a distinct mediad inclination from a point almost opposite the termination of the inner tooth row (Fig. 9, p. 31). As a result, the dental arcade has an approximately horse-shoe shaped outline in occlusal view (a feature not shared with *T. sparrmanii* or *T. ruweti*).

Some growth related dental changes are apparent in the sample studied. The larger specimens usually have very weakly bicuspid teeth (almost shouldered unicuspids) intercalated amongst the true bicuspids, and a few unicuspids occur anteriorly and anterolaterally in both jaws. It is impossible to ascertain whether the shouldered teeth are the result of wear, or are elements in an ontogenetic series; the presence of true unicuspids, however, seems to be explicable on the latter basis.

Inner-row teeth in fishes of all sizes are tricuspid, generally with the cusps of equal size and length, but some do have the centre cusp taller and broader than those flanking it.

Anteriorly, and to a slight extent anterolaterally, the inner teeth are arranged in several series, narrowing to a single row which never extends along the entire length of the outer row.

In fishes 40.0–151.0 mm standard length there are 40–70 (modal range 46–50) outer premaxillary teeth, the number showing no clear-cut correlation with the individual's size, although the highest number occurs in the largest specimen examined. The number of inner rows, however, does show some positive correlation with size; the largest specimens (140.0 and 151.0 mm S.L.) have, respectively, six and five rows in the upper jaw and six and four in the lower jaw. Smaller fishes (n = 20) have 3(f4), 4(f10) and 5(f6) rows in the upper jaw, and 3(f9), 4(f8) and 5(f3) in the dentary.

PHARYNGEAL JAWS AND DENTITION. When *in situ*, the upper pharyngeal bones have the typical tilapiine cardiform outline (see Greenwood, 1987, fig. 4).

The lower pharyngeal bone has a short keel, its length contained 2.5–3.0 times in the length of the dentigerous area, the latter being as broad as it is long or slightly broader than long. When viewed ventrally, much of the body of the bone underlying the dentigerous surface has an inflated appearance (Fig. 4).

The lower pharyngeal teeth are closely and regularly arranged, especially over the posterior third of the dentigerous area. Most teeth are of the typical tilapiine 'kukri' form (Greenwood, 1987: 196–7; fig. 30), with the depth of the 'blade' reduced in teeth on the posterior quarter of the bone. Only those teeth in the posterior three or four transverse rows are bicuspid, but the minor cusp is small and in the form of a short, compressed ridge at the base of the major cusp. The latter is tall, with a weak, anteriorly directed curvature.

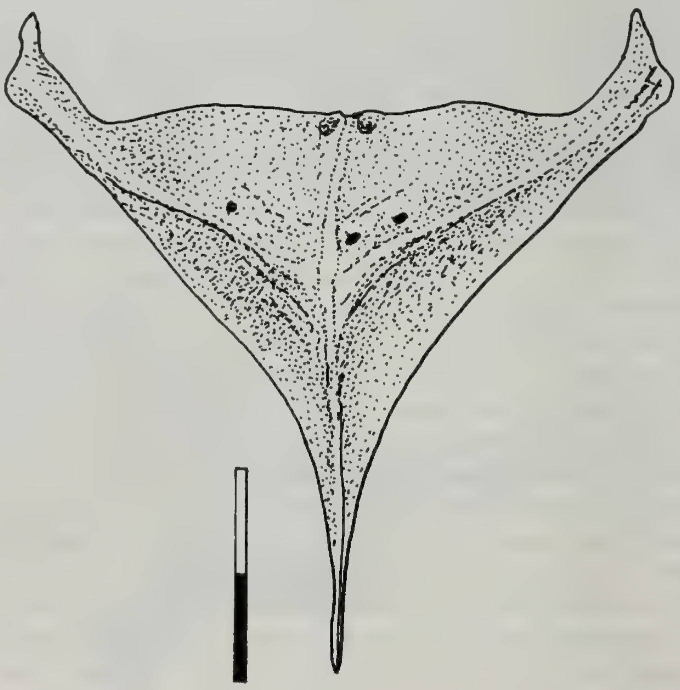

Fig. 4. *Tilapia guinasana*. Ventral aspect of the lower pharyngeal bone. Specimen from the paralectotypical series, BMNH 1935.3.20: 33–51; 70.0 mm S.L. (colour in life unknown, but probably light blue). Scale = 2 mm. Drawn by Gordon Howes.

In their overall morphology, the pharyngeal jaws and dentition of *T. guinasana* are typical for the species comprising Section I of Thys' (1968) tilapiine classification.

NEUROCRANIUM. Data on the neurocranium were derived mainly from five wild-caught specimens representing the colour morphs 'light blue' (2 specimens), 'olive', 'dark blue' and 'large black', covering the size range 45.0–135.0 mm S.L. (neurocranial lengths 12.0–31.5 mm). Additional information, used in the Discussion (p. 35), was obtained from a number of smaller, laboratory-raised fishes.

Osteologically, the neurocranium (Figs 5–8) is probably the most outstanding feature of *T. guinasana*, both when compared with the neurocranium of comparable sized specimens of other *Tilapia* species (*sensu* Trewavas, 1983), and with the skull in *Oreochromis* and *Sarotherodon* species as well (see also Discussion, p. 35). No skeletal material of *Danakilia* was available for comparison.

In particular, *T. guinasana* differs, apparently uniquely, in the appearance of its dorsicranium (Figs 5–8). This is especially noteworthy for the thickness of the frontals, the cambered surface of the supra- and interorbital regions of those bones, the convex rather than concave surfaces of the parietal and supraoccipital between the base of the supraoccipital crest and the fronto-parietal crest, and in the convex surface of the parietal between its contribution to the fronto-parietal crest and the bone's suture with the pterotic. The general appearance of these skull regions in *T. guinasana* is thus one of moderate inflation and roundness, especially when compared with the skull roof in *T. sparrmanii* of a similar size.

Superficially, the greater part of each frontal's dorsal surface (except for the low median crest and the bone's narrow supraorbital margin) has an inflated appearance and, when the skull is viewed from in front, a noticeable, mediolaterally directed camber; in other *Tilapia* species this area is either flat or slightly concave. The camber is most marked in the smallest skull (12.0 mm neurocranial length) and least obvious in the largest one (31.5 mm Ncl.). This region of each frontal is distinctly ornamented with short, low, often curved, confluent and somewhat randomly orientated ridges as well as with horizontally directed, cave-like pits (Figs 6–8). Such ornamentation was not seen in any other tilapiine skull examined.

When illuminated from below, the frontal gives the appearance of having trapped in it a large number of air or oil bubbles, and when sectioned it has a rigid but sponge-like texture between its inner and outer faces of compact bone (Fig. 8). This hyperdevelopment of spongy bone is partly responsible for the frontal's inflated appearance, and entirely responsible for its relative thickness. Similar spongy bone occurs in the epiotic.

The cambered, convex curvature of the frontal's upper surface is apparent, sometimes to an even more marked degree in other tilapiines, but, however, only when skulls

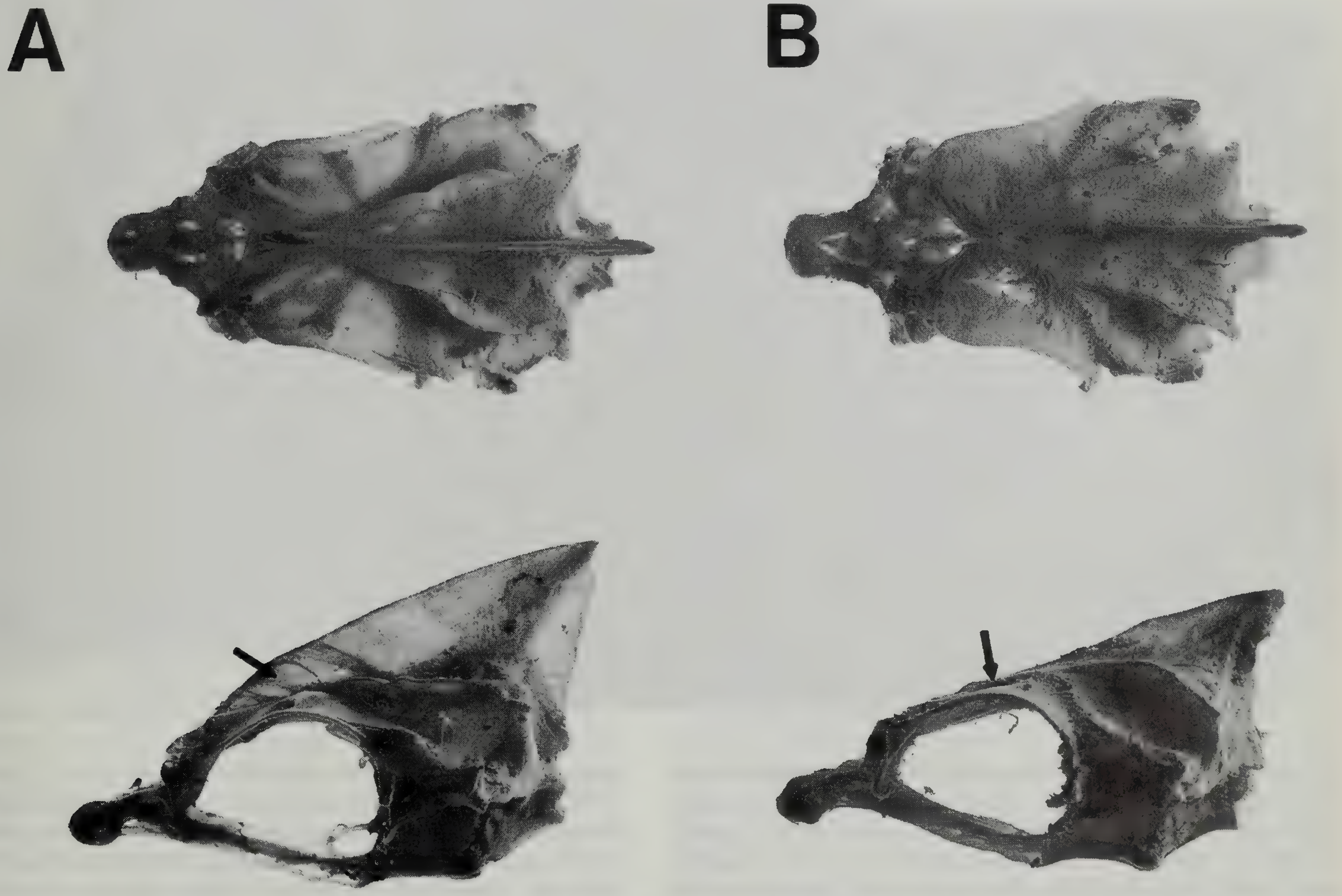

Fig. 5. A. *Tilapia sparrmanii*. Neurocranium in dorsal and in left lateral views. The prominent median frontal crest is arrowed. Specimen from RUSI lot 24197 (Okavango delta), 82.0 mm S.L., neurocranial length 20.0 mm. Magnification ×3.
B. *Tilapia guinasana*. Neurocranium in dorsal and in left lateral views. The low median frontal crest (arrowed) is barely visible above the frontal's dorsal surface; the basisphenoid was lost during preparation of the skeleton. Specimen from RUSI lot 35864 (dark blue), 78.0 mm S.L., 18.0 mm neurocranial length. Magnification × 3.2.

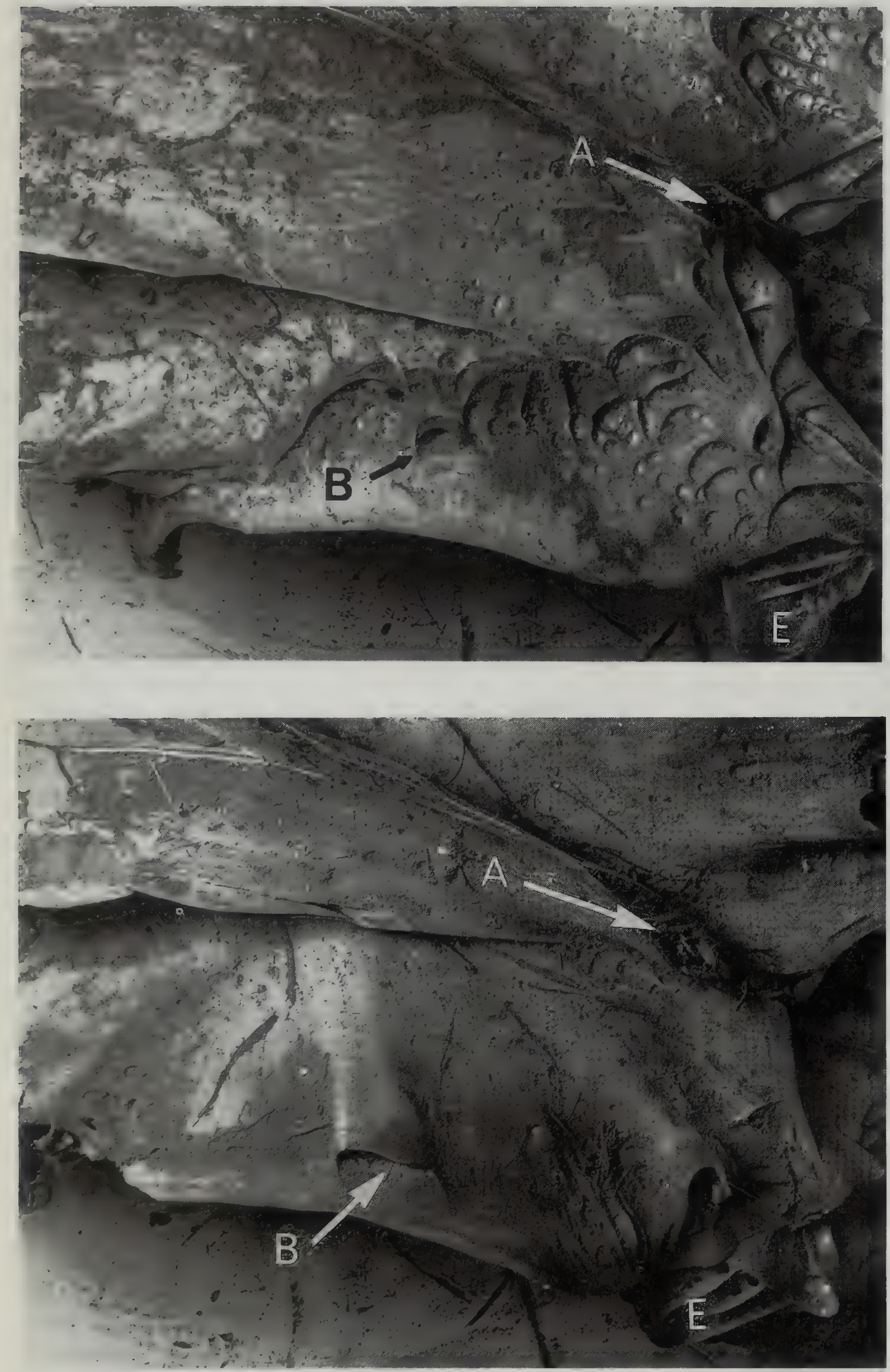

Fig. 6. A. *Tilapia guinasana*. Dorsal view of right frontal (greater part) and a small area of the left frontal showing ornamentation of the bones. Specimen orientated with the midline at 30° to horizontal, anterior is to the right. Arrow A indicates the coronary pore of the cephalic lateral-line system, and arrow B the right supraorbital pore of that system; E: right lateral ethmoid. specimen from RUSI lot 35865 (light blue), 76.0 mm S.L., 18.0 mm neurocranial length. Magnification × 8.
B. *Tilapia sparrmanii*. Comparable area of the dorsicranium. Arrows and abbreviation as in Fig. 6A. specimen as in Fig. 5A. Magnification × 8.

smaller than those of the wild-caught *T. guinasana* specimens are examined. (It is also more marked in the smaller, laboratory-raised *T. guinasana* studied, see p. 35). Unlike *T. guinasana*, none of the other tilapiine species examined shows the spongy hyperosteosis characterizing the frontal and epiotic in that species. The 'rounded' appearance, found only in the juveniles of the other tilapiines, is thus attributable entirely to the shape, at that stage of their ontogeny, of the bones involved. Questions raised by frontal hyperosteosis and the curvature of the bone's dorsal contours in adult *T. guinasana* are discussed in detail later (p. 35).

The orbital face of the frontal is smooth and the bone compact. When viewed laterally there is no marked invasion of the orbit by the ventral surface (Figs 5A & B) of that bone. In other words, the 'inflation' of the frontal is directed dorsally.

Apparently as a consequence of this inflation, the cephalic lateral-line tubules, except for their pores, are not readily visible as intrusions onto the frontal's surface, as they are in other *Tilapia* species except *T. ruweti* (which does not,

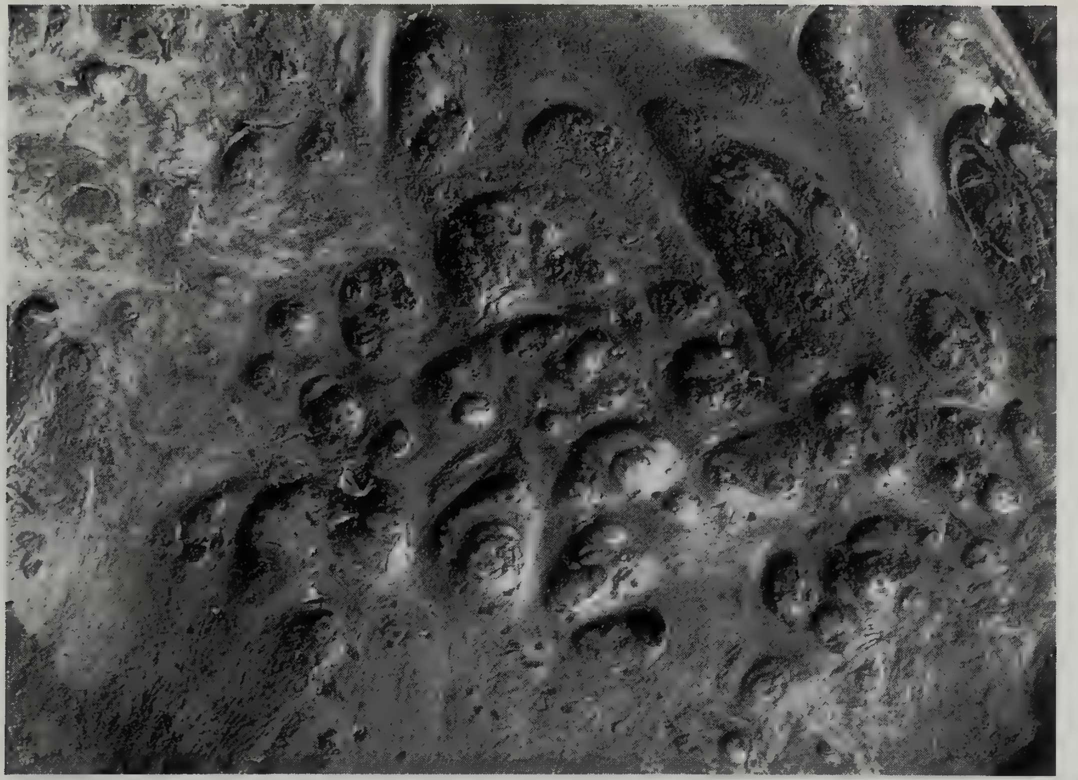

Fig. 7. *Tilapia guinasana*. Rugose ornamentation on the right frontal in the area between the origin of the frontal's contribution to the frontoparietal crest and the supraorbital opening of the cephalic lateral-line system. Specimen as in Fig. 5B. Magnification × 36.

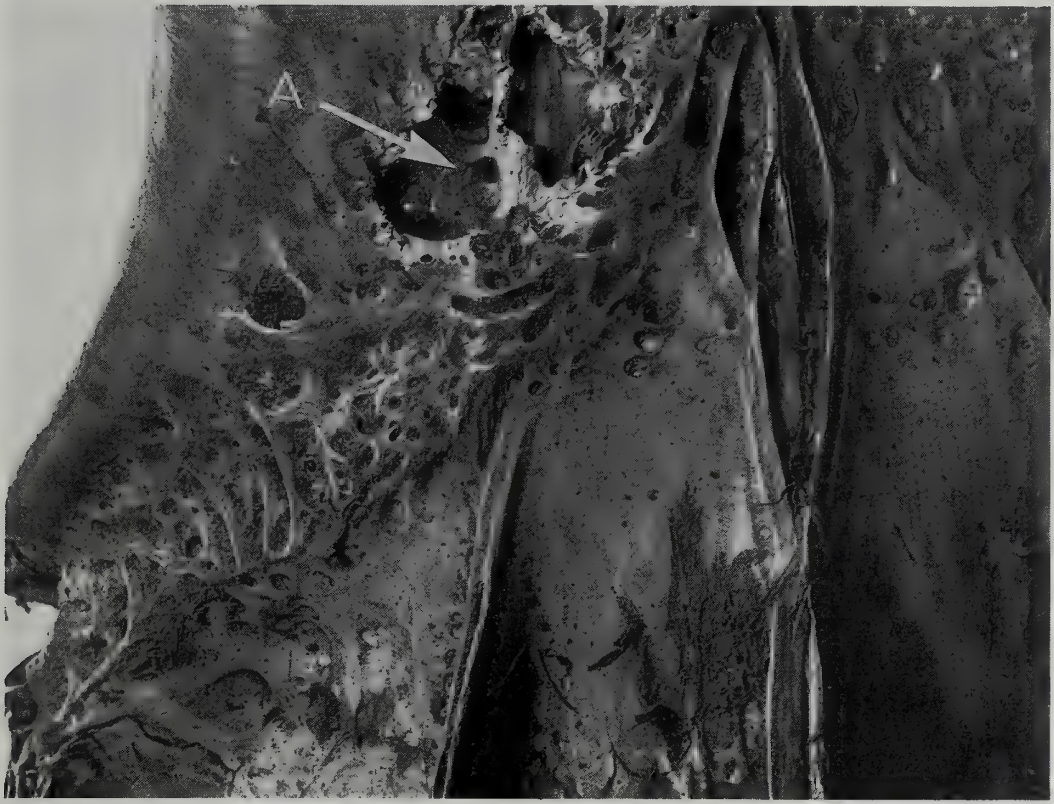

Fig. 8. *Tilapia guinasana*. Posteromedian area of the frontals to show their ornamentation. The ridge situated over and partly anterior to the laterosensory canal opening into the infraorbital canal (see this page) is clearly visible on the left frontal.

Immediately anterior to this ridge, part of the compact superficial layer of bone has been removed to reveal the spongy bone (arrow A) intercalated between the upper and lower layers of compact bone.

Skull orientated so that the vomer points to twelve o'clock. Specimen as in Fig. 5B. Magnification × 12.

however, show any inflation of its frontals).

Except in the largest skull there is little development of the median frontal crest formed along the suture line between the left and right bones and which continues forward the anterodorsal outline of the supraoccipital crest. Even in the largest *T. guinasana* skull the crest is relatively lower than that in comparable-sized neurocrania of other *Tilapia* species, especially *T. sparrmanii* (Fig. 5). A reduction of the crest's height in small specimens, relative to that in larger ones, is, however, a feature of all the small *T. sparrmanii* skulls examined (the only species for which an adequate growth series was available).

Another unusual and probably unique feature of the frontal in *T. guinasana* is the development of an obvious, sometimes prominent, and slightly curved ridge running on or a little anterior to the passage through that bone of the lateral-line tubule opening into the infraorbital canal series (Fig. 8). The ridge originates on the frontal below and contiguous with the frontal portion of the fronto-parietal crest slightly anterior to its suture with the parietal portion. It runs parallel to, and in contact with the crest for a short distance, then curves sharply laterad and downwards towards the opening of the tubule. The ridge is best developed in the larger skulls.

The fronto-parietal crests are relatively low and are of variable anterior extent. In four skulls (12.0–19.0 mm Nc.l.) the crests extend to the level of the supraorbital pore of the frontal lateral-line tubule; over their entire length the crests incline a little towards the midline (and one another) but do not meet medially. The fifth, and largest skull (31.5 mm Nc.l.), has more prominent crests that are more medially inclined and contact the median frontal crest a little posterior to the coronary lateral-line pore.

In the absence of much information about variability in fronto-parietal crest prominence, and their anterior extension and alignment in *Tilapia* species, little importance can be attached to the situation in *T. guinasana*. However, personal observations show that in this species and *T. sparrmanii* all three conditions are similar, but in *Tilapia ruweti* from the Okavango system the crests are lower than those in *T. guinasana* and converge anteriorly but do not meet the median frontal crest.

The supraoccipital crest is variable in its outline, and differs little from that in *T. sparrmanii*. Its height, expressed as a percentage of neurocranial length, ranges from 27.5 to 34.6%. When viewed laterally, however, the crest appears to be less expansive and shorter than in *T. sparrmanii*. This impression is a consequence of the low and short median frontal crest in *T. guinasana*. The longer and more prominent crest in *T. sparrmanii* continues forward the dorsal outline of the supraoccipital crest, thus seeming to increase both the latter's area and its anterior extent. A similar apparent shortening of the crest occurs in *T. ruweti*, and for the same reasons as in *T. guinasana*.

In an early paper considering intragroup relationships of the then single genus *Tilapia*, Trewavas (1973: 20–23) paid considerable attention to the spatial relationships of the mesethmoid (supraethmoid) and vomer. From her study, Trewavas concluded that the majority of species referrable to her revised *Tilapia* concept (*op. cit.*: 20) had the supraethmoid contacting the vomer, with, in a very few exceptional cases the contact being confined to one side only. In contrast, relatively few (*viz*. 5) *Tilapia* species, and all the *Sarotherodon* species she examined, had the vomer free from the supraethmoid. Two of the five *Tilapia* species in this group, however, had a unilateral contact between the bones.

Trewavas (*op. cit.*) put forward a possible functional explanation for this dichotomy in supraethmoid-vomer relationships. Namely, that the separation of the bones was a consequence of the broader head in *Sarotherodon* species, a proportional change that evolved in association with predominantly microphagous feeding habits and, concomittantly, a reduction in the stresses and strains on that region of the skull in these fishes as compared with the situation in, for example, a piscivore. No explanation, however, was given for the exceptional *Tilapia* species (see above). In a later discussion, Trewavas (1983), cited several exceptions to that supposed correlation, and pointed out a number of cases amongst the Cichlidae where the existence of a supraethmoid free from the vomer must be considered as evolutionary convergences.

A study of the vomer-supraethmoid condition in specimens of *T. guinasana*, and a number of other *Tilapia* species, leads me to suggest that the nature of the bones' relationships could have an ontogenetic basis and thus be correlated with the size of the specimen in relation to the maximum size reached by individuals of a particular species.

In wild-caught *T. guinasana* examined, there is no contact between the bones in three specimens (45.0, 76.0 and 78.0 mm S.L.), slight contact in a fourth (73.0 mm S.L.) and substantial contact in the largest fish, 135.0 mm S.L. There is no contact in the four laboratory-raised specimens of 44.5 to 65.0 mm S.L. Likewise, no contact occurs in four *T. sparrmanii* 41.0–65.0 mm S.L., partial and unilateral contact in one of 80.0 mm S.L., and bilateral contact in a fish of 92.0 mm S.L. All these were wild-caught fishes and each came from a different locality. Trewavas (1973: 22) records that the bones are in contact in this species, but gives no sizes for the three specimens she examined.

A similar size-related correlation exists in *T. rendalli*, a species which Trewavas (*op. cit.*) lists, again without length data, as having the vomer and supraethmoid in contact. In the 40.0, 80.0 and 87.0 mm S.L. specimens I examined the bones are free from one another, but in a specimen of 215.0 mm S.L. there is contact like that in the 200.0 mm fish illustrated by Trewavas (1973: fig. 13).

The largest of the *T. ruweti* I examined (65 mm S.L.) has the bones separated.

That, in tilapiine fishes the relationships of the two bones may not always be correlated with absolute size is, however, suggested by a lack of contact in individuals of several *Sarotherodon* species (some now included in the genus *Oreochromis*; see Trewavas 1983) of a size larger than individuals of those *Tilapia* species in which the bones are in articulation, as for example in the *Oreochromis shiranus* examined and figured by Trewavas (1973: fig 14A). In these exceptional taxa it would seem that either the juvenile condition is retained in fully adult and large fishes, or the onset of articulation is delayed until a growth point nearer the modal maximum length for the species is reached. Further research is needed before a clearer understanding of the phenomenon is obtained and its phylogenetic significance, if any, can be determined (for comments on the latter issue, see Trewavas, 1973 and 1983).

Apart from its characteristic dorsicranial morphology, the skull of *T. guinasana* shows no outstanding or unique features. Its overall proportions are of the generalized *Tilapia* type, as are its articulatory apophysis for the upper pharyngeal bones, and the well-ossified lateral commissure of the *pars jugularis* (Greenwood, 1986).

JAWS. There are no species-specific characteristics associated with the upper jaw bones. The dentary, however, does depart somewhat from the usual *Tilapia* condition (Fig. 9). Before curving medially, the lateral aspects of this bone, at a point slightly below its dentigerous surface, have a distinct outward bulge, as does that region of the bone forming the lower limb of the indentation which receives the anguloarticular. As a result of this curvature, the lower part of the dentary has a rather bullate appearance, especially when compared with its counterpart in *T. sparrmanii*. In *T. guinasana*, the dentary's ventral profile also slopes more steeply upwards than in *T. sparrmanii*, a difference which seems to enhance the bullate appearance of the entire bone in *T. guinasana*.

When compared with the dentary in some but not all specimens of *T. sparrmanii*, the bone in four of the five *T. guinasana* examined has a relatively greater mediad expansion of its dentigerous surface anteriorly and anterolaterally. In these specimens, this expanded, ventrally sloping and cliff-like area also has a rather inflated appearance. Both features are less marked in the fifth skeleton, prepared from a 'large black' individual, 135.0 mm standard length.

The exceptional *T. sparrmanii* specimens also show an

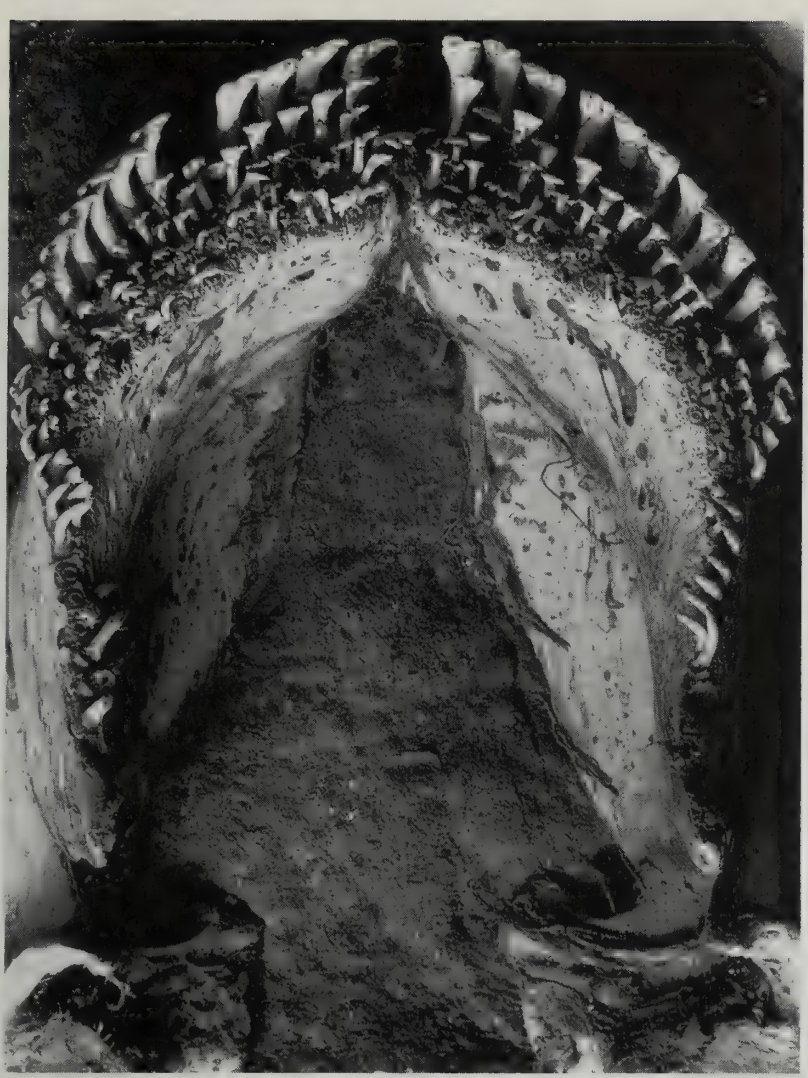

Fig. 9. *Tilapia guinasana*. Lower jaw in occlusal view to show the 'horseshoe'-shaped dental arcade, the unicuspid teeth situated posteriorly in the outer tooth row of the dentary, and the anterior, lingually directed, cliff-like expansion of that bone. Specimen from RUSI lot 35865 (dark blue), 76.0 mm S.L. Magnification × 10.

expanded area like that in the smaller *T. guinasana*, but it does not have the same inflated appearance in this species. Judging from the *Tilapia* material studied, a marked and distinct expansion of this region of the dentary is not a common feature; it is not developed in either *T. ruweti* or *T. rendalli*, the two taxa for which material was available covering, *in toto*, the same size-range as the *T. guinasana* examined.

In the *T. guinasana* and *T. sparrmanii* examined the size of the expanded area is correlated with the number of inner tooth rows present, being widest in specimens, of both species, with the highest (and numerically comparable) number of rows.

INFRAORBITAL BONE SERIES. The series is complete (that is, six elements including the lachrymal and dermosphenotic) in all but one of the five *T. guinasana* skeletal preparations. In the exceptional fish there are only five elements on one side, apparently as a result of fusion between the third and fourth bones. This specimen is also exceptional in having four (not five) openings to the lateral-line system in both lachrymal bones; all other specimens, including the type-series and the specimens used in this paper, have the usual number of five.

VERTEBRAL COLUMN. There is a total, including the urostylar centrum, of 25(f2), 26(f17) or 27(f2) centra in the specimens radiographed (including the holotype), comprising 12(f14) or 13(f7) abdominal and 12(f1), 13(f6), 14(f13) or 15(f1) caudal elements. Where it could be identified on the radiographs, the spondylophysial process is on the third vertebra. A single supraneural (predorsal) bone is present.

CAUDAL FIN SKELETON. Judging from the 20 radiographs in which the caudal fin skeleton is clearly visible, there is a marked tendency for its upper elements, including the epurals, either to be fused, partially fused or closely apposed to one another. In nine specimens the 3rd and 4th hypurals are fused into a single plate, and in ten others these bones are either partially fused or in very close apposition. In eight fishes only a single epural is visible. From its size, it would seem to represent a fusion of the usual two bones.

There is no suggestion that fusion of either the hypurals or the epurals is more, or most, frequent in any one particular colour morph, and in no specimen are the two lower hypurals closely apposed to one another.

Little published information is available on the caudal osteology of tilapiine fishes (Vandewalle, 1973; Trewavas, 1983). Based on that information and on personal observations, it seems that fusion of the epurals, or their reduction to a single element in some other way, has not been recorded previously. Hypural fusions, in various combinations have, however, been recorded.

OTHER OSTEOLOGICAL FEATURES. The palatoquadrate arch, the suspensorium, opercular series, hyal bones and the branchial skeleton in *T. guinasana* do not depart in any outstanding way from the supposed generalized condition seen, for example, in *Tilapia sparrmanii*. However, the dorsoposterior margin of the suboperculum in *T. guinasana*, unlike that in *T. sparmanii*, slopes forwards (it is vertical in *T. sparrmanii*); as a result, there is a distinct excavation in the posterior margin of the opercular flap at the point where the operculum and suboperculum are in articulation (see also p. 33).

COLORATION. Detailed descriptions of the live colours in the five principal and four subsidary morphs (p. 22) are given by Ribbink *et al.*, (1991).

Preserved coloration is extremely varied. The dark blue and olive morphs (p. 22) range from uniformly light- to dark-charcoal and black. One specimen (dark blue in life) is a blotched grey-brown overlying a yellowish ground colour on the flanks, almost uniformly dark charcoal on the dorsal surfaces of the head and body, and yellow with a few dark blotches on the ventral and ventrolateral aspects of the head, chest and anterior part of the belly. Traces of spaced vertical bars are faintly visible on the flanks and caudal peduncle of lighter coloured individuals, and all fins are dusky or black.

Preserved light-blue morphs are a less intense version of the blotched dark blue fish described above, with the yellow colour extending further over the head and along the belly to about the level of the anus. In lighter individuals, the dark pigment on the flanks appears to be concentrated into spots at the scale centres, the area around the spots being much lighter and greyish in colour. All fins, including the pelvics, are greyish-yellow.

The enigmatic 'large' fishes (see p. 22) are represented in the collection by two colour forms. Three specimens, including the fish identified as olive when alive, are uniformly and intensely black on the head and body; the fins, including the pectorals and pelvics are black basally but shade to charcoal-grey distally. The other large fish, classified when alive as '?Light blue', is coarsely blotched, black on yellow, with yellow lips and lower jaw, and all fins, except the pectorals and pelvics dark over most of their length but lightening to yellow near their tips. The pectorals are black basally but otherwise greyish, the pelvics black except for their yellowish tips.

No 'Tilapia-mark' is visible on any of the preserved specimens, wild-caught or laboratory-raised, over 52.0 mm S.L. In one laboratory raised fish, 44.5 mm S.L., a definite mark was present, and in another, 50.0 mm long, the dorsal fin has three, small, comma-shaped and serially arranged dark spots in the region of the fin where a 'Tilapia'-mark should occur.

The loss of a 'Tilapia mark' at such a small size contrasts strongly with the situation in *T. sparrmanii* where, amongst the populations I examined, a fully developed mark is retained in sexually active fishes of much larger sizes (see also Jubb, 1967).

DIAGNOSIS

In the original diagnosis for *T. guinasana*, Trewavas (1936) compared the species only with *T. sparrmanii*, the geographically nearest *Tilapia* species and also the one most closely resembling the new taxon. Since 1936 another species of the group (*sensu* Thys, 1968) to which both *T. guinasana* and *T. sparrmanii* belong, has been described, namely *T. ruweti* (Poll & Thys, 1965), and must be included in any diagnosis.

Tilapia guinasana is immediately distinguishable from both species on the basis of its polychromatism (a feature of which Trewavas was unaware) and the fact that none of its colour morphs resembles the adult coloration in either of the other two species. The juvenile coloration, especially of the body, does, however, approach that in some colour phases of *T. sparrmanii* adults (but not sexually active individuals) and juveniles. (Personal observations on aquarium specimens of both species, the *T. sparrmanii* being wild-caught individuals from the Okavango delta, and the *T. guinasana* wild-caught fry subsequently raised in aquaria at the J.L.B. Smith Institute).

Although superficially *T. guinasana* and *T. sparrmanii* are similar in gross appearance, the former has an obviously more linear and less decurved dorsal head profile, and the upward slope of its lower jaw is less marked.

Trewavas (1936) lists a number of morphometric features separating the two species, but current knowledge of intraspecific variability indicates that none can be considered as critically diagnostic. Nevertheless, although there is an interspecific overlap in ranges for body depth and length of lower jaw (Thys, 1964; personal observations on South African and Okavango specimens), the mean body depth in *T. sparrmanii* is greater than that in *T. guinasana* (42.6–52.1, M = 45.8% of S.L., cf. 36.4–46.6, M = 40.0% for the species respectively), and the mean lower jaw length is greater in *T. guinasana* than in *T. sparrmanii* (33.3–39.1, M = 35.2% head length, cf. 28.4–33.3, M = 31.2%).

Oosthuizen *et al.*, (1991) note that the most outstanding morphometric difference between the species is in the ratio of head width to standard length (35.3% S.L. in *T. guinasana*, 15.9% S.L. in *T. sparmanii*). Regrettably, the authors neither state how head width was measured, nor give the size of the samples measured, and neither is a list of study material provided. Assuming their measurement is the usual one, then the figure for *T. guinasana* can only be a *lapsus* or a typographical error. On the basis of my material there is little difference between the species in the ratio head width/standard length (modal figures 17.0% S.L. and 17.5% S.L. for *T. guinasana* and *T. sparrmanii* respectively). That point apart, I would agree with Oosthuizen *et al*'s conclusion that differences in other morphometric characters are insufficient to separate the two species, and that differences in their meristic features are also inadequate for that purpose, the more so since environmental factors could influence the phenotypic expression of such features.

Body scales are generally larger in *T. guinasana* than in *T. sparrmanii* (lateral scale count 24–27, mode 26, cf. 26–29, mode 28; circumpeduncular count 12, rarely 13, cf. 16, rarely 14 or 15 in *T. sparrmanii*). The scales are markedly rugose in *T. guinasana*, but only slightly so in *T. sparrmanii*, and are thicker in *T. guinasana* (but see Discussion, p. 35). Trewavas (1936) indicates that there are usually fewer rows of cheek scales in *T. guinasana* than in *T. sparrmanii*, but she was misled (see p. 25) in her counts by the deeply embedded lowermost row in the former species (another feature distinguishing the two taxa).

There is an interspecific overlap in the total dorsal fin-ray counts for *T. guinasana* and *T. sparrmanii* but a slight difference in the modal number of rays (25 cf. 23 or 24 for the species respectively). Likewise there is an overlap in the number of spinous dorsal rays (13–15 in *T. sparrmanii* cf. 11–14 in *T. guinasana*) but the mode, 13, is lower in *T. guinasana*.

Another feature used in the original diagnosis, the supposed greater number of tooth rows in the upper jaw of *T. guinasana* (4–7 cf 3 or 4, rarely 5 in *T. sparrmanii*) is no longer effective when fishes over a wide size-range are compared and when *T. sparrmanii* from populations other than those used by Trewavas (1936) are examined.

The short, near pyrimidal gill-rakers (p. 25) are diagnostic for *T. guinasana*.

The nature of the pharyngeal dentition and the overall shape of the lower pharyngeal bone are very similar in both species, but the bone in *T. guinasana* in clearly more bullate ventrally than it is in *T. sparrmanii*.

Some of the various neurocranial features discussed on pages 27–30 would seem to be diagnostic for the species, at least over a certain size-range. Differences in the cambering of the frontals, and the superficial visibility of the lateral-line canals in that bone are, however, less diagnostic when skulls of *Tilapia guinasana* 45–78 mm S.L. are compared with those of *T. sparrmanii* specimens less than 40 mm S.L. Again, when the largest *T. guinasana* skull (from a fish 135.0 mm S.L.) is compared with skulls of *T. sparrmanii* specimens over 50 mm S.L., the differences are also less marked. Nevertheless, even in the latter comparison, the relevant areas of the frontals in *T. guinasana* have a somewhat more inflated appearance than do their counterparts in *T. sparrmanii*.

The very poorly developed median frontal crest (p. 28) of *T. guinasana* in the size range 45–78 mm S.L. is comparable with the condition found in the skull of a 41 mm S.L. *T. sparrmanii*, but not with the prominent crest in larger specimens of that species; even in the largest *T. guinasana* skull examined the crest is relatively lower and less prominent than in any *T. sparrmanii* skull from specimens over 40 mm S.L.

The possible significance of these size-related differences, and of the other departures from the *T. sparrmanii* condition in the skull of *T. guinasana*, are discussed in more detail later (p. 34).

Consistent differences in the skulls of the two species, irrespective of an individual's size, are the relatively inflated epiotic in *T. guinasana*, the hyperosteosis and sponginess in parts of the frontal, (p. 27), the rugose and pitted surface of that bone, and the presence of a prominent ridge above or close to the cephalic lateral-line tubule opening into the infraorbital part of that system.

Throughout the size-range of skeletal material examined, the lateral aspects of the dentary and anguloarticular bones in *T. guinasana* are distinctly more bullate than those in *T. sparrmanii*. A buccally directed, cliff-like expansion of the inner aspect of the dentary is also developed in *T. sparrmanii*, but apparently only in specimens having higher numbers of inner tooth rows on that bone; it is, however, never as prominent as the mental thickening in *T. guinasana*. Unlike *T. guinasana*, the dental arcade of the dentary in *T. sparrmanii* does not have a horse-shoe shaped outline but conforms to the more usual U-shaped condition.

Vertebral numbers in the two species overlap (25–27 in *T. guinasana*, 26–28 in *T. sparrmanii*), although the modal number is lower (26) in former than in the latter (27).

In addition to marked differences in their live coloration, and the absence of polychromatism in *T. ruweti*, the latter species differs from *T. guinasana* in several other respects. Superficially, *T. ruweti* has a more slender body-form, a rounded dorsal head profile, and its caudal fin is distinctly rounded, more obviously so than in the few *T. guinasana* with a caudal margin approaching that condition.

The body scales in most specimens of *T. ruweti* are slightly smaller than in *T. guinasana* (26–28, mode 28 in the lateral series, cf. 25–28, mode 26 for the species respectively) as are those around the caudal peduncle (14–16, mode 15, cf. 12 in *T. guinasana*). There are, modally, more rows of cheek scales in *T. ruweti* (3, rarely 2, cf. 2, rarely 1 in *T. guinasana*); although in *T. ruweti* the lowermost scale row is not deeply embedded in the skin, it can easily be overlooked because it is almost completely overlain by the row above it. An unusual feature in the squamation of *T. ruweti* not shared with *T. guinasana* is the presence of a single scale between each of the lateral-line pores on the horizontal arm of the preoperculum; these scales are deeply embedded in the skin and are not visible without dissection. As compared with the scales in *T. sparrmanii*, especially on the body, those of *T. ruweti* have a more rugose central area, but the roughness is less marked than in *T. guinasana*, and the scales are also thinner and thus like those of *T. sparrmanii*.

Apart from the distinctly rounded caudal fin in *T. ruweti*, there are no other diagnostic features in the fins of the two species.

Gill-rakers in the outer series of the first gill-arch in *T. ruweti* are quite unlike those in *T. guinasana*, being finer and lanceolate, and having low and fine marginal serrations. The rakers are usually fewer in number (8 or 9) than in *T. guinasana* (8–10, rarely 11, mode 10).

When the neurocrania of comparable sized (ie. 47–65 mm S.L.) individuals are compared, the skull of *T. ruweti* is, in general, more like that of *T. sparrmanii* than that of *T. guinasana*, especially in the absence of any spongy hyperosteosis of the frontals, and the absence of a ridge above or close to the cranial tubule linking the cephalic and infraorbital lateral-line systems. Nevertheless, there are certain skull features resembling or approaching those developed in *T. guinasana*.

For example, the cephalic lateral-line tubules, except for that connecting the supraorbital pore with the main canal, are almost as indistinct, superficially, as are those of *T. guinasana*. Also, the area of the frontals between their lateral crests and the midline has a somewhat convex surface, albeit one less cambered than in *T. guinasana*, and the median frontal crest is as poorly developed as it is in comparable-sized individuals of *T. guinasana*.

The lower pharyngeal bone has proportions similar to those in *T. guinasana* (and *T. sparrmanii*), and its ventral surface shows a degree of bullation intermediate between that of the two species. The lower pharyngeal teeth are fewer and coarser than in *T. guinasana* (and also *T. sparrmanii*).

There are no specifically diagnostic features in the oral dentition of the two species, except that the lower dental arcade in *T. ruweti* does not have the near horse-shoe shaped outline characterizing the arcade in *T. guinasana*. The dentary itself is less bullate in *T. ruweti*, and the buccally directed mental thickening is not well developed.

Unlike *T. sparrmanii* but as in *T. guinasana*, the upper part of the subopercular posterior margin in *T. ruweti* has a distinct anterior inclination (see p. 31).

Based on figures given in Trewavas (1983) and a radiograph of 33 *T. ruweti* specimens from the Okavango delta, total vertebral counts in the two species overlap (26–28 in *T. ruweti*, 25–27 in *T. guinasana*), but the modal number is higher (27) in *T. ruweti*, than in the latter species (26), as is the modal number of abdominal centra (13 cf. 12 in *T. guinasana*). No epural fusion was noted amongst the Okavango *T. ruweti* radiographed.

DISCUSSION

The uniqueness of *T. guinasana*'s extensive, non-sexlimited polychromatism amongst tilapiine cichlids, indeed amongst any African taxon of that family, requires no further comment (see p. 22). Regrettably, nothing definite can be said about its evolution or its genetical basis.

It seems reasonable to assume that the founder population, whether it reached Lake Guinas by surface or subterranean means, was small and thus that the polychromatism may be a consequence of this and perhaps other genetical bottlenecks in its history. Since sexual dichromatism does not appear to be part of the specific mate recognition system (*sensu* Paterson, 1985) in the genus *Tilapia*, there is, on that account, no reason why the alleles for different colour morphs should not spread through the population. Nor are there any obvious grounds for their being selected against or, for that matter, having a positive selective value (see p. 34).

Since polychromatism is known amongst other African and New World cichlids (Fryer & Iles, 1972; Greenwood, 1981; Barlow, 1976; 1983), albeit in a far more restricted way than in *T. guinasana*, its occurrence in that species is itself not exceptional, although 'aberrantly' coloured specimens of other *Tilapia* species have rarely been recorded. Indeed, the only published account I have found is of a blotched gold and black form of *Tilapia rendalli* from lake Kariba (Kenmuir, 1983: plate 32); unfortunately, no record is given of its frequency in that lake. Nor has polychromatism ever been described from any populations of *T. sparrmanii*, including those occupying isolated sinkholes (eg. Wondergat in the Transvaal, RSA) or springs (such as Kuruman Eye, northwestern Cape province and Molopo Oog, western Transvaal, RSA).

It has been suggested (Skelton, 1989) that '. . . this spectacular explosion of colour forms . . .' in *T. guinasana* may be explained by the species, or its founders, having been present in a subterranean waterbody before it became a sinkhole. Consequently, '. . . in total darkness the genetic control over colour was lost'. Alternatively, Skelton (*op. cit.*) postulates that '. . . in the absence of competition or predation from other fish species, especially closely related species, there was little need or selection for a distinctive coloration for mate recognition, general communication or for camouflage purposes' (see also Penrith, 1978).

Because sexual dichromatism is not a characteristic of the specific mate recognition system in *Tilapia* species (see Trewavas, 1983), one of Skelton's four suggestions would seem to be negated. The existence of equally un-camouflaged colour morphs, and indeed brightly coloured breeding male cichlids in the clear waters of Lake Malawi, where predators abound (Fryer & Iles, 1972; Ribbink *et al.*, 1983), at first sight weakens any explanation based on selection for camouflaging coloration, although the absence of cover in Lake Guinas, when compared with Lake Malawi, could be a factor supporting Penrith's and Skelton's suggestion.

The importance of colour in communication, particularly at the interspecific level, is difficult to assess in the evolutionary and especially selectionist context under consideration. That it is important intraspecifically, at least for certain species, is well-established (see discussion in Fryer & Iles, 1972). It would seem in the case of *T. guinasana* adults that its role has been considerably diminished, but no research has been undertaken on that point. However, Ribbink (personal communication) did observe that in five of the principal colour forms, the coloration was expressed with different intensities and apparently related to differing emotional states. Those observations also appear to undermine Skelton's argument.

In the absence of any information on the genetical basis for polychromatism in *T. guinasana*, it is not possible to comment on Skelton's (*op. cit.*) views regarding polychromatism and the subterranean origin of the species, although in other cave or grotto-dwelling fishes (including a New World cichlid; Hubbs, 1938) the trend is towards loss or reduction of colour rather than an elaboration of patterns and pigments.

The other unique features of *T. guinasana* are concerned mainly with the cranial skeleton (see pages 27–30). In particular these involve the thickened and spongy nature of much of the frontals, the pitted and rugose ornamentation on those bones, the development of a ridge associated with the cephalic lateral-line tubule running into the infraorbital canal, and the inflated epiotic bone. Nothing approaching these features was seen in any of the other *Tilapia* species examined, nor were any found in the various *Oreochromis* and *Sarotherodon* species studied, which included all the taxa living in the thermal soda-lakes of East Africa (see Trewavas, 1983: 32–35).

In specimens of *T. guinasana* between 45 and 78 mm S.L., the somewhat inflated appearance imparted to the dorsicranium by the thickened frontals is enhanced by their generally convex rather than flat or even concave surfaces such as occur in comparable sized specimens of other species. This impression of a rounded or noticeably cambered surface in *T. guinasana* is reinforced by the fact that the cephalic lateral-line tubules, even in specimens larger than 78 mm, are sunken into the bone and do not break its surface contours. That condition, however, also occurs in *T. ruweti*, although it was not seen elsewhere in the genus.

The impression of a gently cambered dorsicranium in *T. guinasana* is less marked, however, when the largest skull (from a fish 135 mm S.L.) is compared with equal-sized neurocrania of *T. sparrmanii* (and other species, too). Furthermore, when comparisons are made between the skulls of small (ie. 41.0–45.0 mm S.L) *T. sparrmanii* and those of *T. guinasana* between 45 and 78 mm S.L. it is apparent that, although the small *T. sparrmanii* skulls do not show any hyperosteosis of the frontals, their dorsicrania have a cambered, gently convex appearance closely approximating to that of the *T. guinasana* skulls. Also, the *T. sparrmanii* skulls, when compared with those of larger conspecifics, show a proportional decrease in the height and extent of the median frontal crest, relatively lower fronto-parietal crests, and cephalic lateral-line tubules which are barely visible on the surface. In these characteristics the small *T. sparrmanii* skulls resemble closely skulls from larger *T. guinasana* specimens, although the curvature and generally domed appearance of the dorsicranium is more marked in the 45 mm *T. guinasana* than it is in the 45 mm specimens of *T. sparrmanii*.

This level of similarity between the skulls of small *T. sparrmanii* and those of considerably larger *T. guinasana* individuals suggests that, in many respects, the latter have retained, even into sexual maturity, the juvenile skull morphology of other tilapiines. The fact that the skull of the largest *T. guinasana* examined is more like that of a *T. sparrmanii* less than half its length, seems also to support the idea of delayed neurocranial morphogenesis in *T. guinasana*, at least with respect to the fish's standard length (the ages of the specimens being unknown).

To test that idea, the skull of a 38.0 mm S.L. *Tilapia zillii* (neurocranial length 10.5 mm) was compared with a *T. zillii* skull of 37.5 mm Nc.l (from an individual of unknown standard length), and with skulls from *T. sparrmanii* 41.0 mm S.L. (Ncl 11.0 mm), 80.0 mm S.L. (Nc.1 20.0 mm) and 92.0 mm S.L. (Nc.l. 21.0 mm).

The areas of marked frontal cambering (and hence a domed appearance) in the small *T. zillii* skull (10.5 mm Nc.l) are almost identical with the similar-sized skull (11.0 mm Nc.l) of *T. sparrmanii*, but the median frontal crest in the former is lower, the cambering of the frontal medial to its contribution to the fronto-parietal crest is more pronounced, and the crest is lower. In those respects, the dorsicranium of the *T. zillii* skull is even nearer the usual adult condition in *T. guinasana* than is the similar sized skull of *T. sparrmanii*. When the dorsicrania of *T. sparrmanii* 80.0 and 92.0 mm S.L. (Nc.l 20.0 and 21.0 mm respectively) are compared with the largest *T. zillii* skull (Nc.l 37.5 mm), no obvious differences were noted, suggesting that in both species similar ontogenetic form-changes were involved, and that the skull in adult *T. guinasana* does retain certain features characteristic of much smaller individuals of *T. zillii* and *T. sparrmanii*.

Similar conclusions regarding ontogenetic changes in skull form were reached when the skulls in several alizarin preparations of laboratory spawned and reared *Oreochromis mossambicus* were compared with adults of the species and with the skulls of juvenile and adult *Tilapia sparrmanii, T. zillii* and *T. guinasana*.

In the small *O. mossambicus* (16.0–18.0 mm S.L.) the cambering of the dorsicranium is so pronounced that its entire dorsal surface could be described as domed. It is without traces of the gulley between the supraoccipital crest and the region which will be occupied by the still undeveloped fronto-parietal crests, no or virtually no median frontal crest is present, and only the lateral-line tubule connecting with the infraorbital tubule is visible on the surface of the dorsicranium; the other cranial tubules, however, are faintly visible below the surface. In other words, the situation in these small *O. mossambicus* represents a more extreme form of that seen in *T. guinasana* 45.0–78.0 mm S.L. Since, in its overall appearance, the dorsicranium in adult and subadult *O. mossambicus* is closely similar to that in adult *T. sparrmanii* and subadult and adult *T. zillii*, one can conclude that all three species undergo similar ontogenetic form-changes which are not completed in *Tilapia guinasana* of a comparable size. The condition seen in the largest *T. guinasana* skull examined (neurocranial length 31.5 mm, from a fish 135.0 mm S.L.) suggests that even individuals of this size do not develop a skull-form free of juvenile features already lost in *T. sparrmanii* one third of their length.

One can, at present, only speculate on the causal, perhaps epigenetic, mechanism or mechanisms resulting in the *T. guinasana* condition. One such sequence of events may involve the hyperosteosis and consequent thickening of the frontals constraining and influencing ontogenetic changes in the shape of the bones. Hyperosteosis is manifest in the smallest wild-caught *T. guinasana* available, but in the absence of even smaller specimens its first appearanc ein ontogeny could not be ascertained.

If hyperosteosis is involved, then an explanation is required for the seemingly restricted occurrence of the phenomenon, not only to *T. guinasana* but also its restriction to the scales and certain skull elements, in particular the frontals, part of the supraoccipital, the parietals and the epiotics of that species.

One possible explanation for the occurrence of hyperosteosis in *T. guinasana* is that of environmental induction. Lake Guinas water has a very high calcium carbonate content (calcium hardness, as $CaCo_3$, 185 ppm), an environmental factor to which the fishes might have responded, physiologically, by increasing the volume and calcification of certain bones. If that is so, the particular sites of hyperosteosis (which also include the thickened scales; p. 25) still require explanation.

Without attempting to draw any conclusions on these issues, some observations on four laboratory spawned and raised *T. guinasana* may be relevant. The specimens are part of an F1 generation, derived from wild-caught parents kept, subsequent to their capture, in Grahamstown tap-water (calcium hardness, as $CaCO_3$, *ca.* 45 ppm) in which the young were also raised.

In all four fishes the overall morphology of the dorsicranium is nearer that of similar sized wild-caught *T. sparrmanii* than of *T. guinasana*. The roofing bones involved (p. 27) are thinner and less spongy than in wild conspecifics, and there is a noticeable reduction in the pitting and rugosity of the frontals. The scales in these specimens, especially in the two larger fishes, are thinner and less rugose than in specimens from Lake Guinas, and the body of the lower pharyngeal bone is less bullate (p. 26). Interestingly, however, the morphology of the dentary, and the shape of its dental arcade (p. 30) are identical with those of wild-caught *T. guinasana* and thus are noticeably different from the condition seen in *T. sparrmanii*.

It is planned to carry out, in the near future, experiments aimed at clarifying the extent to which such environmental factors as water chemistry may influence the structure of certain skull roofing bones and in turn influence the morphology of the dorsicranium in both *T. guinasana* and *T. sparrmanii*.

A close phyletic relationship between *T. guinasana* and *T. sparrmanii* was suggested by Trewavas (1936) on the grounds of both species having low numbers of gill-rakers, dorsal fin spines and scale rows on the cheek. On that basis, *T. ruweti* (Poll & Thys, 1965) could also be considered a close relative, the more so since it shares with *T. guinasana* certain features not found in *T. sparrmanii* (p. 33). However, because no fully cladistic phylogenetic analysis is available for the tilapiines it is impossible to assess the polarity of the features shared by the two taxa. Outgroup comparisons with other labroids and within the tilapiines (*sensu* Trewavas, 1983 but excluding the pelmatochromines and chromidotilapiines of Greenwood, 1987), strongly indicate that, on the basis of breeding habits and the nature of the pharyngeal dentition, the genus *Tilapia* is the most pleisiomorphic member of the tilapiines (data from Trewavas, 1983; Thys, 1968, and personal observations). Within that genus, and because of their relatively coarse pharyngeal dentition with bicuspid teeth posteriorly on the lower bone, and their low vertebral numbers, *T. sparrmanii*, *T. ruweti* and *T. guinasana* are probably the least derived species (data sources as above). Within that trio of species, the unique polychromatism of *T. guinasana* (and possibly its unusual osteological features) give it a derived status, as do certain features of *T. ruweti* (see p. 33), whilst *Tilapia sparrmanii*, with its generalized syncranial osteology seems to be the most plesiomorphic form.

There is some doubt about the genetic rather than ecophenotypic basis for certain of the apparent osteological autapomorphies characterizing *T. guinasana* (see discussion above), but no doubt can be entertained about the uniqueness of its polychromatism.

Unequivocal synapomorphies shared by *T. guinasana* and either *T. ruweti* or *T. sparrmanii* cannot be identified at present. Consequently, sister species are unidentifiable and the presumed close relationship between *T. guinasana* and *T. sparrmanii* can only be considered conjectural. The overall superficial similarity between the two species has also led to arguments, mostly unpublished, that *T. guinasana* should not be treated as a distinct species, but rather as a variant population of *T. sparrmanii* (see discussion in Skelton, 1988).

As with all disjunct populations there is no adequate way of establishing the existence, or otherwise, of intrinsic barriers to successful genic exchange between *T. guinasana* and *T. sparrmanii*, and thus determining their status as biological species. On the other hand, the apparently absolute physical isolation of *T. guinasana*, taken together with the autapomorphic characters it exhibits, qualify it for the status both of a phylogenetic species (*sensu* Cracraft, 1989) and of an evolutionary species (*sensu* Wiley, 1981). Thus in my view, its specific status cannot be doubted, a conclusion also reached by Oosthuizen *et al.*, (1991) on the basis of their biochemical studies.

APPENDIX

Tilapia guinasana in Lake Otjikoto

The first transfer of *T. guinasana* to Lake Otjikoto, another sink-hole lake with similar water chemistry, some 50 km east of Lake Guinas, is recorded as taking place in 1922, (see p. 21) but it may not have been successful since, when Jordan's party visited the lake in 1931 and collected fishes there, no *T. guinasana* were included amongst the material studied by Trewavas (1936); see also Penrith (1978); and Skelton (1988; 1989). However, the species is now well established in the lake.

Only four preserved specimens of Otjikoto *T. guinasana* were available for study; all are adults in the size range 74.5–86.0 mm S.L. A cranial skeleton was prepared from the 75.5 mm specimen.

In all morphometric and meristic features, these specimens lie within the ranges for fishes from Lake Guinas, and in no morphological or dental features, including the shape of the dental arcade of the lower jaw (see p. 30), do they differ from the parental stock. However, the Otjikoto individuals all have a circumpeduncular scale-count of 13, a figure rarely recorded from the Guinas sample, and the rugosity of their body scales is less marked.

The skull shows no clear-cut departure in its gross morphology from those of Guinas specimens, although the frontal rugosities and pitting are less pronounced and fewer in number.

It is not possible to determine live colours from the preserved material, but Dr Ribbink and Ms Twentyman-Jones (personal communications) have seen representatives of the light blue and olive morphs, and a striped form, when diving, in poor visibility, in Lake Otjikoto.

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A revision and redescription of the monotypic cichlid genus *Pharyngochromis* (Teleostei, Labroidei)

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Synopsis. Since its original description by Boulenger in 1911, *Pelmatochromis darlingi* Blgr (1911), now the type and only species of the genus *Pharyngochromis* Greenwood (1979), has not been fully revised despite the greatly increased amount of material now available from an extensive area of Africa. The type specimen is from the Zambezi river system, but subsequent material has been collected, from several localities, in the upper, lower and middle reaches of the Zambezi as well as from the Okavango and Save-Runde systems, and the Quanza system in Angola.

A wide but intergrading range of intraspecific variability is revealed when material from these areas is examined, and it appears that three other species *viz. Chromis jallae* Blgr (1896), *Pelmatochromis multiocellatus* Blgr (1913) and *Chromis acuticeps* Steindachner (1866), all currently of uncertain generic and specific status, are conspecific with *P. darlingi*. Because *acuticeps* is the oldest available name, the single component species of *Pharyngochromis* must now bear that name.

Consideration is given to the taxonomic and philosophical problems raised when the various allopatric and often physically isolated populations of *P. acuticeps* are viewed in the light of different species' concepts. No formal taxonomic solution, however, can be found.

The phylogenetic interrelationships of *Pharyngochromis*, especially with regard to the genera *Chetia* and *Serranochromis*, are still obscure. In reviewing that problem, questions are raised about the 'reality' of the taxon *Chetia* now that two further species, *C. mola* Balon & Stewart (1983) and *C. welwitschi* (Blgr) 1898, have been included in it and an earlier view that *Chetia brevis* Jubb (1968) may not be a member of that genus is no longer considered tenable.

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INTRODUCTION

The monotypic genus *Pharyngochromis* was erected by Greenwood in 1979 for Boulenger's species *Pelmatochromis darlingi*, at that time referred to the polyphyletic genus *Haplochromis* as delimited by Regan in 1922 (see Greenwood, *op. cit.*). The phylogenetic affinities of *Pharyngochromis* apparently lie with the southern African group of haplochromine genera characterized by simple, non-ocellar and usually numerous spots on the anal fin of males (and often females as well) and by the presence of only cycloid scales or a predominance of such scales on the flanks (Greenwood, 1979: 274–5; 311–12).

Since Boulenger's original description of *P. darlingi*, based on the holotype alone (a fish from the Makabusi river, Zimbabwe), there have been numerous other records of the species from Zimbabwe, and its range has been extended to include Angola and the Okavango system in Botswana (Regan, 1922; Barnard 1948a; Poll, 1967; Jubb, 1967; Jubb & Gaigher, 1971; Skelton *et al.*, 1985; Bell-Cross & Minshull, 1988).

Although both Regan (1922) and Poll (1967) have given either a partial redescription of the species, or published meristic and morphometric data for material from a particular locality, there has been no complete redescription incorporating material from the entire range of the species as presently known. This paper is an attempt to rectify that situation and to consider the relationships of *P. darlingi* with certain similar species from Zimbabwe and Angola whose current status, both specific and generic, is uncertain (see Greenwood, 1979: 312–3; 1984: 233–4). In that context particular attention was paid to *Chromis acuticeps* Steindachner (1866) and *Pelmatochromis multiocellatus* Blgr (1913), both from Angola, and the enigmatic *Chromis jallae* Blgr (1896) from Zimbabwe. All three species were placed in the genus *Haplochromis* by Regan (1922).

Information now available on the intraspecific variability of *P. darlingi* populations from the Zambezi, Save-Runde and Okavango systems indicates that this 'species' is conspecific with at least two syntypes of *Chromis acuticeps* and thus becomes a junior subjective synonym of that taxon. My review also indicates that Boulenger's *Chromis jallae* and his *Pelmatochromis multiocellatus* are additional synonyms of *acuticeps*, the latter union already strongly hinted at by Trewavas (1973: 31).

The reasons which I consider warrant the union of these nominal taxa are as follows: 1. The presence of numerous non-ocellate spots (see Greenwood, 1979: 274–5) on the anal fin of at least adult males, and often on that fin in females and juveniles of both sexes as well. The spots show some degree of individual variability in size, number and orderliness of arrangement, but rarely exceed 18 and usually number between 6 and 10.

It was an earlier ignorance of the variability in spot size, number and arrangement manifest amongst the now extensive collections from Okavango and Zimbabwe that led me to doubt Poll's (1967) identification of certain specimens from Angola as *Haplochromis darlingi* (Greenwood, 1979: 311; 1984: 229–230). It was also partly responsible for my uncertainty about the status of *Pelmatochromis multiocellatus*, as it was my view (Greenwood, 1984: 234) that the anal fin markings in the type-specimen were of a true ocellar type. Further detailed examination of the spots shows that they are not true ocelli (ie. with a clear surround, see Greenwood, 1979) and that similar spots, at least in preserved material, occur in specimens previously identified as *Pharyngochromis darlingi* from the Zambezi and Okavango systems.

2. The possession of a relatively enlarged and strong lower pharyngeal bone (manifest even in the smallest specimen examined, 27.5 mm standard length; RUSI 21093), usually with a sinuously interlocking median suture (Fig. 7). The anterior keel of the bone is short and deep, its lowermost point lying somewhat below the level of the bone's main body.

3. At least in specimens over 80 mm S.L. the two median rows of lower pharyngeal teeth are noticeably enlarged and coarse. The posterior pair of teeth in this series is distinctly bicuspid (albeit sometimes weakly so) and the posterior half to two-thirds of each row is composed of teeth either with a slightly rounded and molariform crown, or a flat crown with a low nipple-like cusp situated near its centre (ie. a mammilar crown). In the largest fishes there is a relative increase in the number of enlarged and near-molariform or mammilar teeth, and a few similar teeth also occur in the next lateral row.

Individuals less than 80 mm S.L. have fewer enlarged teeth, most of which are mammilar, in the two median rows, but the other teeth in this series are clearly stouter than their lateral congeners. Some enlarged but usually bicuspid teeth do, however, occur in the next lateral rows. Only in the smallest specimens examined (28–35 mm S.L.) are all the median row teeth distinctly biscuspid, but even in these fishes the teeth are relatively coarser and larger.

4. The last 4–8 (usually 5–7) scales in the upper lateral-line series have one large and one small scale separating them from the base of the dorsal fin (*cf.* species of *Chetia* and *Serranochromis* [*sensu* Greenwood, 1979] where the modal number of such lateral-line scales is 2 or 3).

5. There are 14 (mode) or 15, (rarely 13 or 16) abdominal vertebrae, and 14–16 (mode 15) caudal elements (excluding the fused PU_1 and U_1 centra) giving a total count of 28–31 (mode 30) vertebrae.

In effect, these are the principal characters used to define the genus *Pharyngochromis* (see Greenwood, 1979: 310–311; 316), and I can find no others that would trenchantly separate different species within the material examined. This included the type-specimens of *Chromis acuticeps, Pelmatochromis multiocellatus, Chromis jallae* and *Pelmatochromis darlingi*, large collections of supposedly *Pharyngochromis darlingi* from the Okavango and Zambezi systems and some, but regrettably few, from Angola as well.

None of the features used by Regan (1922) in his key and elsewhere to distinguish between the species *acuticeps, multiocellatus, jallae* and *darlingi* is effective. When large numbers of specimens are examined, all intergrade and no group shows any modal distinctiveness. Even the obliquely truncate caudal fin margin of *P. darlingi* holotype (Fig. 4), a seemingly diagnostic feature, has not been observed in any further specimens referrable to the taxon on other grounds. It is presumably either teratological or the result of *pre-mortem* damage and repair.

As mentioned earlier, this revision is based mainly on characters recorded from preserved specimens, although it has been possible to compare colour notes and descriptions taken from Zambezi, Save-Runde and Okavango populations

(Jubb, 1967: 171, plate 46; Bell-Cross & Minshull, 1988: 248, plate 20 [a reprint of Jubb's plate 46]; Skelton and Greenwood, personal observations). These reveal no apparently significant differences. Regrettably, no data on live colours are available for fishes from other localities. When such information is available and there is more knowledge of other biological characteristics, especially ethological ones, then further division of the now monotypic taxon may be necessary (see Discussion p. 48).

METHODS AND MATERIAL

Method

The systems of counts and measurements are those detailed in Greenwood (1979 and 1984). When making vertebral counts, the last abdominal centrum is identified as that having a pleurapophysis with which a pleural rib articulates (no matter how reduced the rib may be). The urostylar element (the fused PU_1 and U_1 centra) is not included in the count of caudal vertebrae.

Material

Specimen lots that have been radiographed are indicated with a dagger if the plates are in the British Museum (Nat. Hist.) collections, and by an asterisk if held by the J.L.B. Smith Institute of Ichthyology, Grahamstown.

Colour transparencies are held in the J.L.B. Smith Institute, and the original of Hilda Jubb's watercolour painting of a *P. acuticeps* specimen (probably number AMG. P1600 from the Rusawi river, Save-Runde system) is housed in the Albany Museum, Grahamstown.

Institutional abbreviations following Leviton *et al.*, 1985 are: AMG, Albany Museum, Grahamstown; BMNH, British Museum (Nat. Hist.), London; MRAC, Musee Royal de l'Afrique Centrale, Tervuren; MSNTO, Museo Civicio di Storia Naturale di Torino; NMW, Naturhistorisches Museum, Vienna; NMZB, National Museum of Natural History Zimbabwe, Bulawayo; RUSI, J.L.B. Smith Institute of Ichthyology, Grahamstown.

Type material examined

Chromis acuticeps†. Lectotype, NMW 32–877, 3 paralectotypes, NMW 32–878 (Fig.1).
Chromis jallae†. Holotype, MSNTO P–3192 (Fig. 2).
Pelmatochromis darlingi†. Holotype, BMNH 1908.12.11:5 (Fig. 4).
Pelmatochromis multiocellatus†. Holotype, BMNH 1911.6.1:167 (Fig. 3).

Other material

Zambezi system

AMG. P128*. Nampini confluence of Zambezi-Chobe systems.
RUSI. 30121. Kazungula, about 1 km above Katamboro rapids, Upper Zambezi.
NMZB. 3360. Lake McIlwaine (Hunyani river, middle Zambezi).
NMZB. 3490. Caprivi strip, between Chobe and Zambezi rivers.
NMZB. 3930. Kafue river, near Kitwe.
BMNH. 1910.3.7.3.† Maramba river, an affluent to the Zambezi (see Boulenger, 1915).
BMNH. 1919.5.22:1–4†. Sesheke, upper Zambezi.
BMNH. 1937.4.22:99–108†. Balovale (upper Zambezi).
BMNH 1970.6.25:48–50†. Hunyani river (upper Zambezi).
MRAC. 163981–7†. Lake Calundo, Angola (upper Zambezi).

Save-Runde system (Zimbabwe)

AMG. P132*. Macheke river.
AMG. P1600. Rusawi river.

Quanza system (Angola)

BMNH. 1911.6.1:162†. Lucala river.

Okavango system

RUSI 20163 and 22107. Popa rapids, Okavango river.
RUSI 21516. Boro river, Buffalo fence.
RUSI 20722*. Boro river, 5 km upstream of Thamalakane confluence.
RUSI 20610. Nxaraga lagoon, Boro river.
RUSI 34974*. Xakanika lagoon, Maunachira river.
RUSI 21317. Maxegana lagoon, Botletle river.
RUSI 21463*, 34973 and 34976*. Chanoga lagoon, Botletle river.
RUSI 21093*. Third bridge, Sekiri river.
RUSI 23748. Thamalakane river, upstream of Okavango River Lodge.
RUSI 20283*. Okavango river, Mkena.
RUSI 34972. Okavango river, Rundu beach.
The majority of Okavango localities are shown in maps provided by Skelton *et al.* (1985).

A REDESCRIPTION

Pharyngochromis acuticeps *(Steindachner) 1866.*

Figs 1–5

SYNONYMY. Arranged alphabetically under species.
For amplification of entries marked with an asterisk, see notes on pages 40–43.

Chromis acuticeps Steindachner, F., 1866. *Verh. zool.–Bot. Ges. Wien*, **16**: 764, Taf. XV, fig. 2.

Tilapia acuticeps (part): Boulenger, G.A., 1915. *Cat. Afr. Fw. Fish*. **3**: 218–9, fig. 141 (The other specimen, from Kazungula, Upper Zambezi, cannot be located at present).

Haplochromis acuticeps (part): Regan, C.T., 1922. *Ann. Mag. nat. Hist.* (9) **10**: 225 (The type, the specimen from Lucula [see *T. acuticeps* above], and the reference to *Tilapia ramsayi* Gilchrist & Thompson, 1918* [the trivial name *rumsayi* misspelt and the date an error]).

Paratilapia arnoldi Gilchrist, J.D.F. & Thompson, W.W., 1917. *Ann. S. Afr. Mus.*, **11**: 521.

Pelmatochromis darlingi Boulenger, G.A., 1911. *Ann. Mag. nat. Hist.* (8) **7**: 377; *Idem*, 1915. *Cat. Afr. Fw. Fish. 3*: 410,

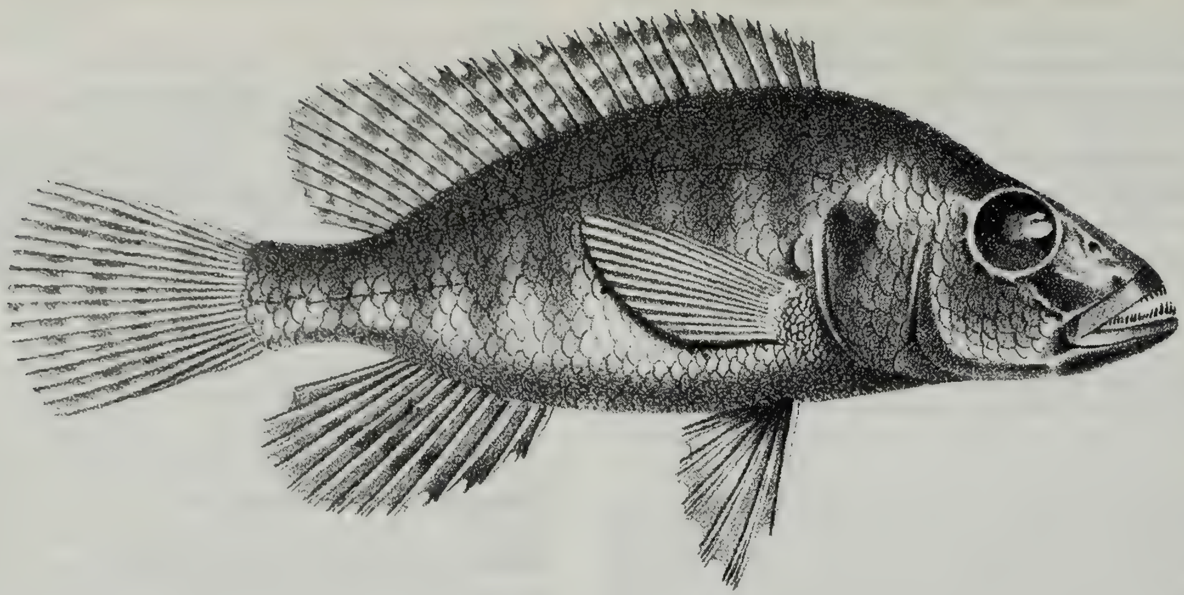

Fig. 1. *Chromis acuticeps* Steindachner. One of the type series; this figure is not positively identifiable with a particular specimen in that series. From Steindachner (186).

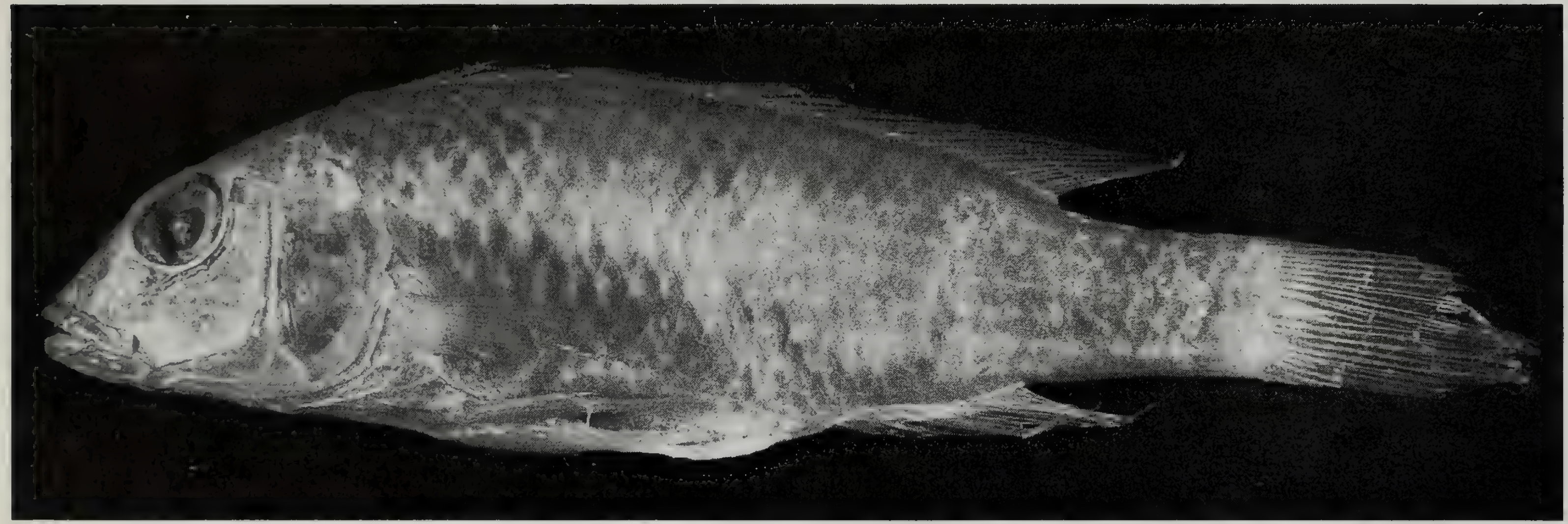

Fig. 2. *Chromis jallae* Blgr. The holotype; S.L. 59.0 mm. Photographed by Robin Stobbs.

fig. 280; Gilchrist, J.D.F. & Thompson, W.W., 1917. *Ann. S. Afr. Mus. 11*: 535.

Haplochromis darlingi: Regan, C.T., 1922. *Ann. Mag. nat. Hist.* (9) **10**: 256; Barnard, K.H., 1948. *Cape Inland. Fish. Dept., report* no. 5: 60. *Idem*, 1948. *Ann. S. Afr. Mus.* **36**: 453.

Haplochromis darlingi (part: excluding *Astatotilapia ellenbergeri** Pell.): Jubb, R.A., 1961. *An illustrated guide to the freshwater fishes of the Zambezi river; Idem*, 1967. *Freshwater fishes of Southern Africa*: 47; Jubb, R.A. & Gaigher, I.G., 1971. *Arnoldia* **5** (7): 20; Jackson, P.B.N., 1961. *The fishes of Northern Rhodesia*: 112; Poll, M., 1967. *Publicoes cult. Co. Diam. Angola* no. 75: 313 (tentatively excluding Pellegrin's [1936] material identified as *Pelmatochromis welwitschi**).

Pharyngochromis darlingi: Greenwood, P.H. 1979. *Bull. Br. Mus. nat. Hist.* (Zool.) **35** (4): 310–11; Skelton, P.H. *et al.*, 1985. *Ichthyol. Bull. J.L.B. Smith Inst. Ichthyol.* no. 50:11.

Chromis jallae: Boulenger, G.A., 1896. *Boll. Mus. Torin* **9**: 260.

Tilapia jallae: Boulenger, G.A., 1915. *Cat. Afr. Fw. Fish.* **3**: 213.

Haplochromis jallae: Regan, C.T., 1922. *Ann. Mag. nat. Hist* (9) **10**: 255; Barnard, K.H., 1948. *Cape Inland. Fish. Dept., report* no. 5:60; *Idem*, 1948. *Ann. S. Afr. Mus. 36*: 477 & 453.

*Haplochromis lucullae**: Trewavas, E., 1973. *Bull. Brit. Mus. nat. Hist.* (Zool.) **25** (1): 31.

Haplochromis moffati (part): Boulenger, G.A., 1915. *Cat. Afr. Fw. Fish.* **3**: 300 (the specimen, no. 43, from the Moramba River, affluent of the Zambezi, only).

Pelmatochromis multiocellatus: Boulenger, G.A., 1913. *Ann. Mag. nat. Hist.* (8) **12**: 484; *Idem*, 1915. *Cat. Afr. Fw. Fish.* **3**: 409–410; fig. 279.

Haplochromis multiocellatus: Regan, C.T. 1922. *Ann. Mag. nat. Hist.* (9) **10**: 256.

NOTES ON SYNONYMY.

1. ?*Tilapia rumsayi* Gilchrist & Thompson, 1917. This species (its entry preceded by an interrogation mark) was first synonymized with *Haplochromis acuticeps* by Regan (1922), who misspelt the trivial name as *ramsayi*. Barnard (1948b) questioned Regan's tentative action on the grounds that the type of *T. rumsayi*, which he, but not Regan, had seen, '. . .

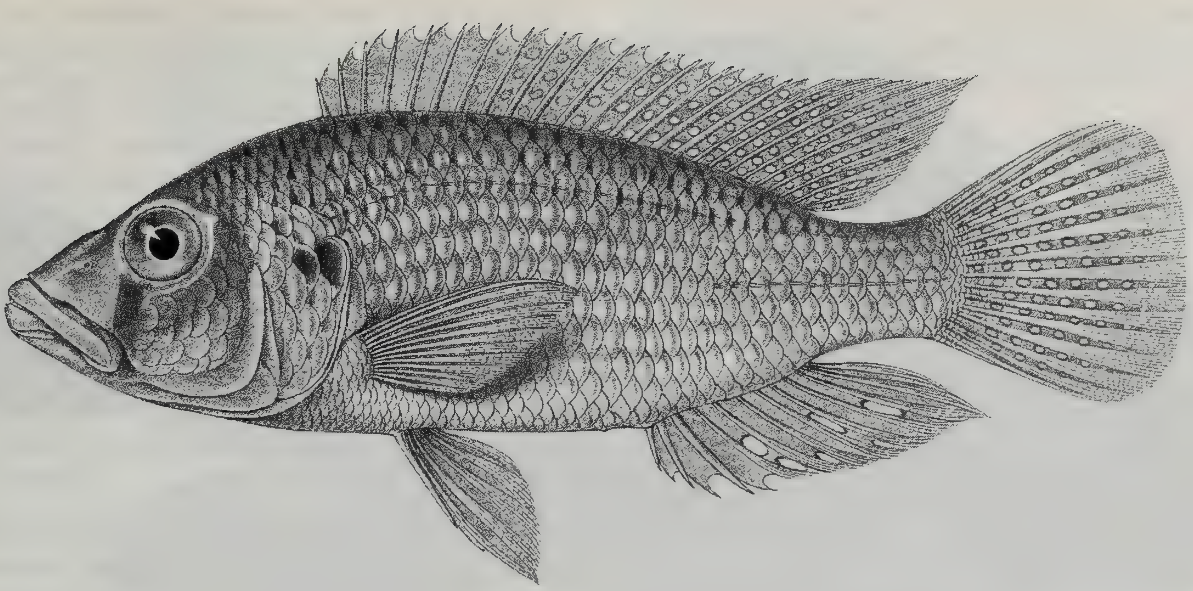

Fig. 3. *Pelmatochromis multiocellatus* Blgr. Holotype; S.L. 97.0 mm. From Boulenger (1915).

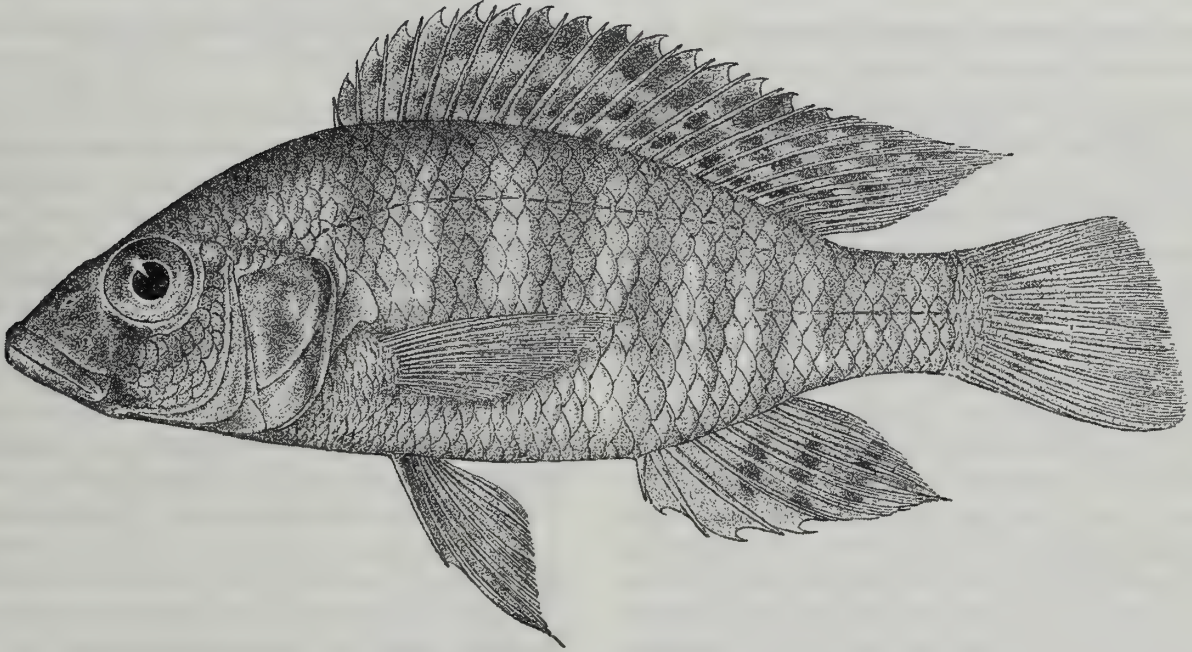

Fig. 4. *Pelmatochromis darlingi* Blgr. Holotype; 84.5 mm. From Boulenger (1915).

has stout and blunt pharyngeal teeth' (*cf*. small, compressed and hooked according to Regan), and thought that the species should be treated as a synonym of *Haplochromis darlingi*. In the same year Barnard (1948a: 447) repeated his doubts, and listed *T. rumsayi* (again preceded by an interrogation mark) as a synonym of *H. darlingi* in a key to the species of that genus (Barnard *op. cit.*: 453).

I would certainly agree with Barnard's action since I cannot accept Regan's differentiation (or at least partial differentiation) of *H. acuticeps* from *H. darlingi* on the basis of differences in their pharyngeal dentition. The median pharyngeal teeth in the lectotype of *Chromis acuticeps* (from an unknown locality in Angola) are comparable both with those in *Pelmatochromis darlingi* holotype and with most other specimens previously identified as *Haplochromis* or *Pharyngochromis darlingi* from the Zambezi and Okavango systems. Furthermore, Regan's other diagnostic criterion for separating *darlingi* from *acuticeps* (the former's greater posterior extension of the maxilla) no longer holds when large samples are examined, and indeed barely holds when the types of the two taxa are compared.

Barnard's synonymy was accepted by later workers (Jackson, 1961; Jubb, 1967; Jubb & Gaigher, 1971; Skelton *et al.*, 1985).

The reason for my uncertainty about including *T. rumsayi* is the doubts I have about the validity, as Gilchrist & Thompson's holotype, of the specimen thought to have that status; *viz* specimen NMZB. 0711 from the National Museums of Zimbabwe's collection.

This fish is in excellent condition; it is accompanied by a label marked 'Holotype' and bearing the legend '*Haplochromis darlingi*, December 1914, Upper Zambezi River just above the Victoria Falls—Upper Zambezi. Collector F. Rumsay'. Clearly it is not the holotype of *darlingi* (which is in the collections of the British Museum [Nat. Hist.]), and there are reasons to doubt that it is really the type of *Tilapia rumsayi* incorrectly labelled as that of *darlingi* (see below), despite the correct locality and collector's data.

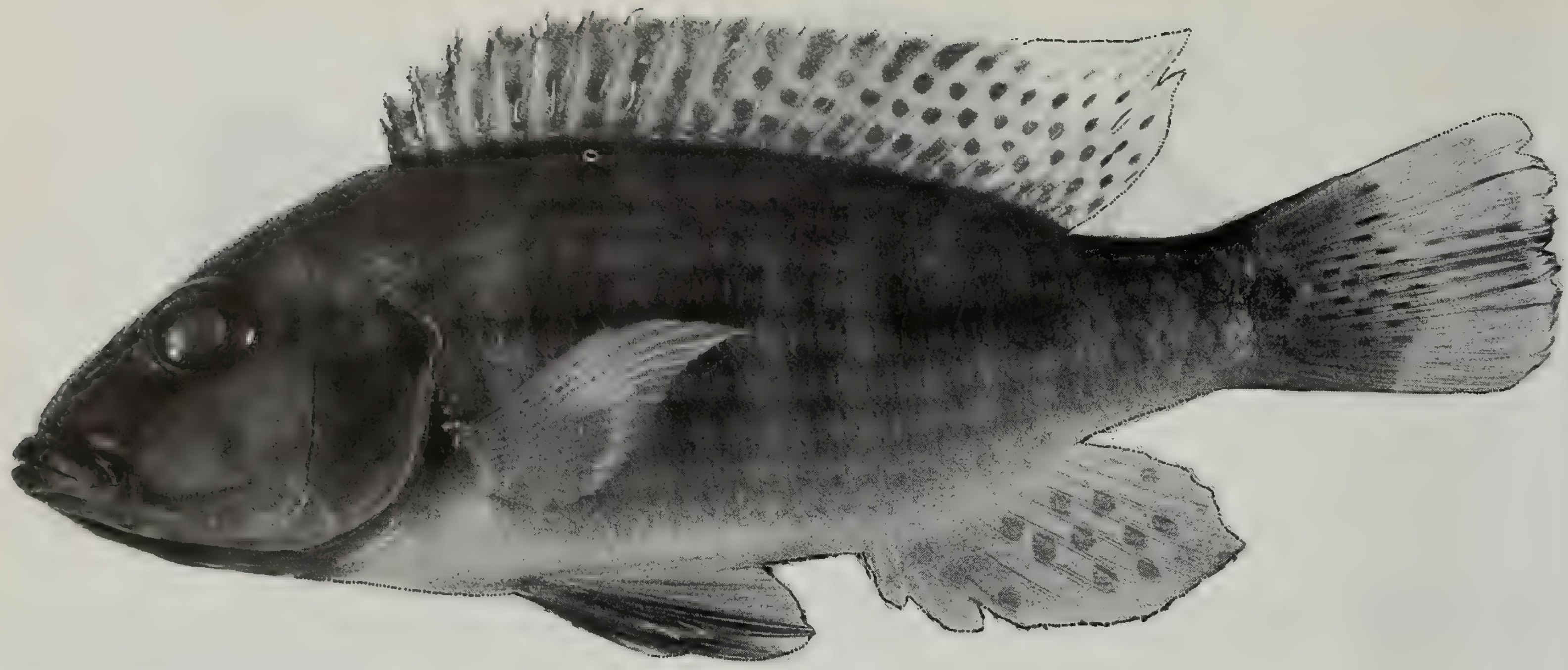

Fig. 5. Pharyngochromis acuticeps (Steind.) Adult male; S.L. 98.0 mm. Okavango system (RUSI 34974). Photographed by Paul Skelton.

According to Gilchrist & Thompson (1917), their specimen was 61 mm in length (whether total or standard length is not specified); specimen 0711 has a standard length of 74.0 mm, and a total length of 95.5 mm. There are other differences too. The original description gives the dorsal and anal fin formulae as XIV 10 and III 6 respectively; the specimen has counts of XV 11 and III 7. Granted, the difference in anal fin branched ray counts may not be significant because the last ray can give the appearance of being a single, deeply divided ray rather than two separate rays. The difference in dorsal ray counts, however, cannot be so easily dismissed.

Then, if Gilchrist & Thompson's figure is accurate (and their description strongly suggests that it is), then the holotype had a far more acute head profile (in lateral view) than has the presumptive holotype whose profile is steeper and more curved, and whose mouth is almost horizontal and not, as figured, sloping at an angle. Finally, the figured specimen also has 14 (and not 15) dorsal fin spines.

In other meristic and morphometric features there are some slight discrepancies between specimen 0711 and Gilchrist & Thompson's description. These may, however, be attributable to differences in our measuring and counting techniques.

It could be argued that Gilchrist & Thompson's published length measurement is a *lapsus*, or perhaps a typographical error, but that would not account for the other differences. Thus, I have grave doubts about the authenticity of specimen NMZB. 0711 as the holotype of *Tilapia rumsayi*, although it certainly seems to be a specimen of *Pharyngochromis acuticeps*.

Unfortunately, further investigations have not located any specimen which can be identified positively as the holotype of *Tilapia rumsayi*, but the search continues (pers. comm., J. Minshull). Nor has it proved possible to discover how the labelling error came about.

2. The exclusion of *Astatotilapia ellenbergeri* Pellegrin (1920) from the synonymy of *H. darlingi* (see synonymies of the latter species by Jubb [1961; 1967] and Jackson [1961]). As far as I can determine, Jubb and Jackson were the first authors to identify *A. ellenbergeri* as a definite synonym of *H. darlingi*. The species was overlooked by Regan (1922), but was noted by Barnard (1948a) as a tentative synonym of *H. darlingi*, possibly the reason why both Jubb and Jackson included it in the synonymy of that species although they made no reference to Barnard's uncertainty of the taxon's true status. Interestingly, neither Jubb (1961; 1967), Jackson (1961), Jubb & Gaigher (1971), nor Bell-Cross (1975, see below) comment on Barnard's other view, also expressed in 1948 (a & b), that the species could be a synonym of *Haplochromis giardi* (Pellegrin), now *Serranochromis (Sargochromis) giardi*; see Greenwood (1979).

In 1975, Bell-Cross included *A. ellenbergeri* in his synonymy of *Haplochromis carlottae* (now *Serranochromis [Sargochromis] carlottae*; see Greenwood 1979), basing that decision on an examination of the holotype. He did not, however, mention the previous inclusion of *A. ellenbergeri* in *H. darlingi*, nor Barnard's (1948 a & b) uncertainties about its identity.

I have examined the holotype of *A. ellenbergeri* and agree with Bell-Cross' decision to include it in *S. (Sargochromis) carlottae* (see also Skelton *et al.* 1985).

3. *Haplochromis darlingi* (?in part); Poll, 1967. The indecision implied by the question mark relates to Poll's inclusion of certain Angolan material identified as *Pelmatochromis welwitschi* by Pellegrin (1936). Pellegrin's description of these specimens is quite inadequate, and none is figured. Until Pellegrin's material can be located and re-examined, both his and Poll's identifications should be treated with caution.

4. *Tilapia jallae* Blgr (1896). This species, known only from its holotype (Turin Museum, P. 3192) has received scant attention in previous accounts of the Zambezi system's haplochromine species. Usually it is merely listed without any comment other than it being known only from one specimen (Regan, 1922; Barnard, 1948 a & b; Jubb, 1961 and 1967). Jackson (1961: 131), however, notes that 'This species, described from the upper Zambezi, is probably not valid, but I am uncertain of its exact status'.

The type is now completely bleached and is in very poor conditions (Fig. 2). Its lower pharyngeal bone and dentition are of the *P. acuticeps* kind, and except for its shallow body (seemingly not entirely an artefact of preservation) its morphometric and most of its meristic features do not serve to distinguish it from comparable-sized specimens of *P. acuticeps*. It is, however, unusual in having 16 rather than 15 (the modal number) caudal vertebrae, and in having 6 rather than 4 or 5 rows (the modal numbers) of scales on its cheeks.

Since the holotype of *T. jallae* is not unique in these departures from the mean or modal conditions, and allowing for its poor state of preservation, as well as taking into account its geographical locality (Victoria Falls district, Zambezi River), I would conclude that it is a slightly unusual specimen of *P. acuticeps*.

5. *Haplochromis lucullae*; Trewavas (1973: 31). I do not agree with Trewavas' identification of this specimen as *H. lucullae*, the one B.M.(N.H.) specimen from the Lucala river which Boulenger (1915: 218) placed in the species *Tilapia acuticeps*. In my view, Boulenger's specific identification was correct since the specimen does not show any of the squamation features characterizing the types of *Tilapia lucullae*, a species now included in the genus *Thoracochromis* (Greenwood, 1979: 290; 1984: 190).

LECTOTYPE. A specimen 59.5 mm standard length (NMW 32–877) from Angola.

DESCRIPTION. Most meristic and morphometric data were taken from 100 specimens 27.5–133.0 mm S.L., including the lectotype and one paralectotype of *Chromis acuticeps* (the others are in a poor state of preservation) and the holotypes of *Pelmatochromis darlingi, P. multiocellatus* and *Chromis jallae*. For some features, fewer than 100 specimens were used when damage, poor preservation or distortion precluded accurate counts and measurements; vertebral counts are based on 68 specimens; this material covers all known localities for the species.

The principal morphometric and meristic features of the various type specimens included in this description are tabulated in the Appendix, as are those for fishes from the Zambezi and the Okavango systems respectively, as well as the Kazungula population (see Discussion, p. 49, with reference to allopatric populations and speciation). Sample sizes of collections from Angola and the Save-Runde system (Zimbabwe) are too small to justify separate tabulation.

Depth of body 27.6–41.1% of standard length (S.L.), with which it shows slight positive allometry; length of head 30.5–37.7 (mean, m, 33.8)% S.L. In both features, *C. jallae* holotype lies at the lower end of the range for specimens of a comparable size.

Dorsal head profile sloping at an angle of 30°–35° to the horizontal, its outline straight or slightly convex posterior to the orbit, straight or gently concave anterior to the orbit and often with the premaxillary ascending processes projecting a little above the rest of the outline. Mouth horizontal or almost so; dorsal outline of orbit coincident with, or a little below the dorsal head profile.

Preorbital depth 14.3–25.6 (m = 20.2%) of head length, showing slight positive allometry with S.L., least interorbital width 14.3–25.6 (m = 19.6)%. Snout length 25.0–37.2 (m = 32.4)% head length (shows slight positive allometry with standard length) and 0.9–1.2 (mode 1.0) times its breadth.

Eye diameter negatively allometric with standard length; in specimens 71.0–133.0 mm S.L. it is 22.2–31.3 (m = 27.7)% head length, and in those 27.5–70.0 mm S.L. it is 27.3–36.0 (m = 31.5)%.

Depth of cheek shows slight positive allometry with standard length; in fishes < 70 mm S.L. it is 16.0–26.2 (m = 21.6)% of head length, and in larger individuals 20.8–28.2 (m = 25.0)%.

Caudal peduncle 1.2–1.8 times longer than deep (modal range 1.3–1.5), with specimens < 80.0 mm S.L. having the deeper peduncles; its length 15.4–21.8 (m = 17.9)% of standard length.

Jaws equal anteriorly, the lower jaw 34.8–48.9 (m = 40.5)% of head length, and 0.9–1.2 times longer than broad. The posterior tip of the maxilla is variable in its posterior extent, rarely reaching the vertical through the anterior margin of the orbit, but usually extending to a point nearer that vertical than one through the nostril. The variability in this character negates Regan's (1922: 253) primary key character for separating *H. acuticeps* from both *H. multiocellatus* and *H. darlingi*.

Gill-rakers. Seven to 12 in the outer series on the ceratobranchial of the first gill-arch, the modal number nine or 10. The rakers are short, stout and cuboidal, those nearest the angle between the cerato- and epibranchial bones sometimes anvil-shaped.

Microbranchiospines are present on the outer face of the second to fourth gill-arches.

Scales. In most specimens, body scales on the flanks below the upper lateral-line, and on the caudal peduncle, are either cycloid or very weakly ctenoid, the ctenii being confined to a narrow median area on the scale's free margin. Such ctenii are rarely well-developed and, as noted before (Greenwood, 1979: 307; 310), their presence is usually most obvious in small individuals.

Some intraspecific variability exists in the size of the chest scales (ie. on the ventral and ventrolateral region of the body anterior to the insertions of the pectoral and pelvic fins). specimens from fast-flowing water tend to have the smallest scales which, in some individuals, are deeply embedded in the skin. However, even in those specimens there is a gradual size transition between the chest scales and those on the ventrolateral aspects of the flanks and belly (*cf.* the condition in *Ctenochromis* and *Thoracochromis* species where the transition is abrupt; see Greenwood, 1979). In all populations, scales forming the median one to three rows on the chest are noticeably larger than those lateral and dorsal to them.

Lateral-line series with 31 to 36 scales (30 in one individual), the modal range being 32 to 34, and the mode 33. The last 4 (rarely) to 8 scales (usually the last 5 to 7) of the upper lateral-line are separated from the dorsal fin base by one large and one small scale.

The cheek has 4 to 6 (rarely 3) rows of scales, with a small but distinct naked area anteroventrally, and sometimes a narrow naked strip between the lowest horizontal row and the lower limb of the preoperculum.

There are 15 (mode) or 16 scales around the caudal peduncle, 4 to 5½ between the lateral-line and the dorsal fin origin, and 5–9 (mode 5) between the pectoral and pelvic fin bases; fishes from rapid waters have the highest counts for the latter character.

Squamation on the caudal fin is arranged in a horizontally aligned and broad-armed 'V', the apex situated at the fin base. Distally, the arms extend to about the mid-point of the fin.

Fins. Dorsal with 14 to 16 (mode 15) spinous and 10 (rarely) or 11 to 13 (rarely 14), modally 12, branched rays. Anal with 3 spinous and 8 or 9 (no distinct mode), rarely 7 or 10, branched rays.

Caudal fin distinctly truncate to almost rounded; the obliquely truncate fin in the holotype of *Pelmatochromis darlingi* (see Fig. 4) has not been encountered in any other specimen, and is probably either teratological or the result of damage and subsequent repair.

The first ray of the pelvic fin is the longest, and is proportionately longer in adult and sexually active males. Pectoral fin length shows some individual variability both as a proportion of head length and its posterior extent relative to the anal fin origin. As a percentage of head length the fin length ranges from 20.2 to 29.8 (m = 25.2); relative to the anal fin origin, it may extend to a vertical passing through any point between the anal fin origin and another passing immediately anterior to the anus. In view of this variability, one of Boulenger's (1915) principal key characters for distinguishing between *Pelmatochromis multiocellatus* and *P. darlingi* (*viz*. for the species respectively, pectoral extends to, or does not reach, the anal fin origin) is rendered invalid. From the sample examined, there is an indication of slight positive allometry between pectoral fin length and standard length, but no correlation was found with sex or sexual maturity.

Teeth. The outer row teeth in both jaws of most fishes < 80 mm S.L. are bicuspid, sometimes weakly so as a result of wear. Some unicuspid teeth may occur in larger individuals within this size range, and become the predominant form in fishes over 90 mm S.L. The number of outer row premaxillary teeth shows some correlation with the individual's size; in specimens over 50 mm S.L. the modal range is 40–50, and the range for the whole sample 24–60.

Bicuspid teeth in *Pharyngochromis acuticeps* have a distinctive but by no means unique form. The neck is relatively stout and the slightly recurved cusps are of markedly unequal size (Fig. 6). The small minor cusp often has an obtusely pointed tip and is sharply angled away from the base of the major cusp. When unworn, the latter has an acute tip and, usually, a low flange or ridge on its posterior margin. The flange occupies about half the height of the cusp, extending from the angle between the two cusps towards the tip of the major one.

Unicuspid teeth are caniniform and moderately stout. The crown, especially of teeth situated anteriorly and anterolaterally in the jaws, is slightly recurved.

Irrespective of their form, teeth in the outer row of both jaws are closely spaced but are never contiguous.

In specimens of all sizes the posterior 1–6 (usually 2 or 3) premaxillary teeth are slender unicuspids, generally smaller than the teeth preceding them. Enlarged and stout caniniform teeth, like those occurring in this position in *Astatotilapia* and some other genera (Greenwood, 1979) are never present in *Pharyngochromis*, a characteristic which this genus shares with *Chetia* and both subgenera of *Serranochromis*.

Inner row teeth in fishes less than 80 mm S.L. are generally a mixture of tri- and bicuspids, the latter often with a 'shoulder' rather than a distinct minor cusp. A few unicuspids may also be present, but rarely are all the inner teeth unicuspid. Larger individuals show a relative increase in the number of unicuspids, and these can be the predominant or even the only form present; however, an admixture of uni- and bicuspids is found in all but the largest fishes (ie. specimens between 100.0 and 136.0 mm S.L.).

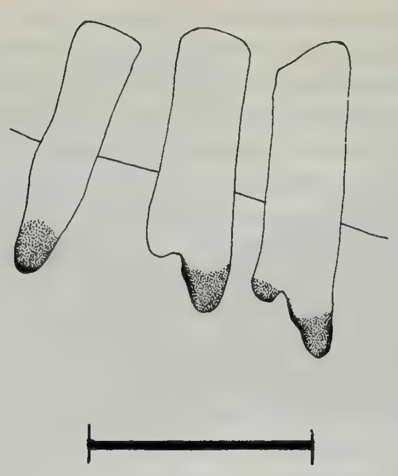

Fig. 6. *Pharyngochromis acuticeps*. Outer row teeth, situated antero-laterally in the right premaxilla. Scale: 1 mm. Drawn by Elaine Grant.

The number of inner tooth rows anteriorly and anterolaterally in the jaws ranges from 1–3 in the premaxilla, and 1 or 2 in the dentary. Only a single row occurs posteriorly and posterolaterally in both jaws. Often the organization of the rows is very irregular, so that it is difficult to differentiate between single and double rows, or between the latter and a triple row condition. Judging from the material examined it seems that the number of premaxillary rows may increase as the fish grows, since single rows occur most frequently in specimens < 80 mm S.L., and double or triple rows in those over 100 mm S.L. The trend is not, however, a clear one and because the sample is biased towards fishes in the smaller size group it may be artefactual.

Lower pharyngeal bone and dentition. The triangular dentigerous surface of the bone is equilateral, its length 65–70% of the bone's overall length. The keel is short (25–27% of the bone's overall length) and deep, with, in most specimens, a distinctly curved ventral outline whose deepest point lies below the lowest point on the ventral surface of the bone's dentigerous part (Fig. 7). An exceptional population, from a farm dam in Zimbabwe, does not have such a deep keel. In these specimens the keel's ventral outline is almost straight and at no point does it lie below the ventral surface of the dentigerous part; the median row of teeth is less hypertrophied and molar-like than in comparable-sized specimens from other populations, and the body of the bone is also less hypertrophied. Judging from those other populations, however, the shape of the keel is not correlated with either the degree to which the pharyngeal teeth are enlarged, or the extent to which the body of the bone is inflated and strengthened.

Apart from the atypical farm dam population, most other specimens, particularly fishes over 40 mm S.L., have the ventral surface of the bone's dentigerous part somewhat inflated and densely ossified. These features are not always proportionately enhanced in large specimens or in those with coarser and more molar-like teeth in the median tooth rows. However, there is a general trend, with growth, towards a more inflated appearance and denser ossification of the

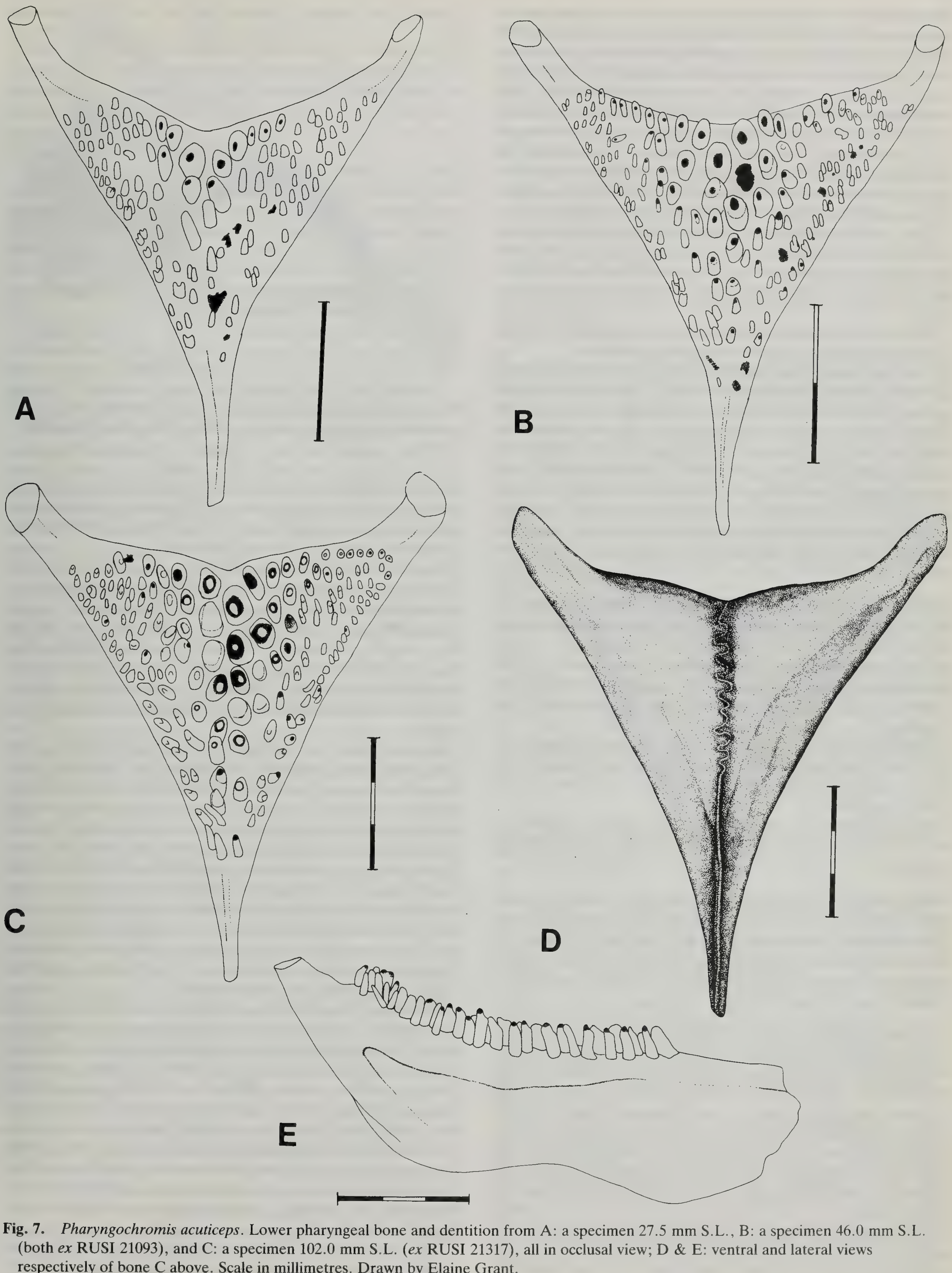

Fig. 7. *Pharyngochromis acuticeps*. Lower pharyngeal bone and dentition from A: a specimen 27.5 mm S.L., B: a specimen 46.0 mm S.L. (both *ex* RUSI 21093), and C: a specimen 102.0 mm S.L. (*ex* RUSI 21317), all in occlusal view; D & E: ventral and lateral views respectively of bone C above. Scale in millimetres. Drawn by Elaine Grant.

dentigerous body. In fishes less than 40 mm S.L. this part of the bone is not noticeably enlarged but above that size, and when compared with, for example, specimens of *Astatotilapia, Chetia* and *Serranochromis (Serranochromis)* species the bone is distinctly coarser and more massive. Indeed, that comparison can be extended to include certain species of *Serranochromis (Sargochromis)* such as *S.(S) gracilis* and *S.(S.) greenwoodi*. In a few individuals of *Pharyngochromis acuticeps* over 75.0 mm S.L., the enlargement can approach or slightly exceed that in comparable sized or even larger *S.(S.) coulteri* (see figs in Greenwood, 1979 and 1984).

The articulatory horns of the lower pharyngeal bone are generally short and stout, but as with the body of the bone (and usually correlated with the degree of hypertrophy in that region) there is some intraspecific variability in their stoutness.

The suture joining the two halves of the bone can be straight and simple, or more often, deeply sinuous.

The lower pharyngeal teeth and changes in their form and size have already been described (see p. 38). It only remains to note that even within one size group, and within a single locality, there is some variability both in the number of enlarged teeth in the median rows and in the degree of molarization shown by these teeth. Greatly enlarged, and much flattened molariform teeth such as occur in many species of *Serranochromis (Sargochromis)*, are not found in *P. acuticeps*, and only rarely are all the teeth in the row next to each median row enlarged with mammilar crowns (see p. 38).

Vertebral column. Counts were obtained from radiographs of 68 specimens, including the lectotype and one paralectotype of the species, and the holotypes of *Chromis jallae, Pelmatochromis multiocellatus* and *Pelmatochromis darlingi*. The geographical range of these various specimens includes the Okavango region, the Zambezi and Save-Runde systems, and Angola.

The total count (excluding the fused PU_1 and U_1 centra) is 28–31 with a distinct mode at 30; it comprises 13 (rare) to 16 (rare), mode 14, abdominal centra and 14–16 (mode 15) caudal elements.

From this sample it was not possible to indicate whether or not any correlation exists between locality and vertebral number.

Neurocranium. There is no intraspecific variability in skull form, which is similar to the neurocranium in *Serranochromis (Sargochromis)* species except that, unlike most members of the subgenus, the neurocranial apophysis for the upper pharyngeal bones is not enlarged in *Pharyngochromis* (see Greenwood, 1979, and Fig. 8).

Coloration. Information is available on live coloration only for specimens from the Okavango swamps (personal observations) and certain localities in the Zambezi and Save-Runde systems (*qv*. Jackson, 1961; Jubb, 1967: 171 and plate 46 [original painting in the Albany Museum]; Bell-Cross & Minshull, 1988: 248 and plate 15, a darkened reprint of Jubb's plate). Since there is apparently no obvious difference in the live colours of fishes from the Zambezi, Save-Runde and the Okavango systems, the description which follows is based on those sources.

The ground colour on the flanks and caudal peduncle in adults and juveniles of both sexes ranges from silvery-grey (darkest dorsally) to pearly blue-grey, with an overlying greenish-golden sheen, and shades dorsally to a darker blue-grey, ventrally to a pearly silver. The cheeks are greenish-golden, and in females and juveniles the branchiostegal membrane is pearly silver, the lips greyish.

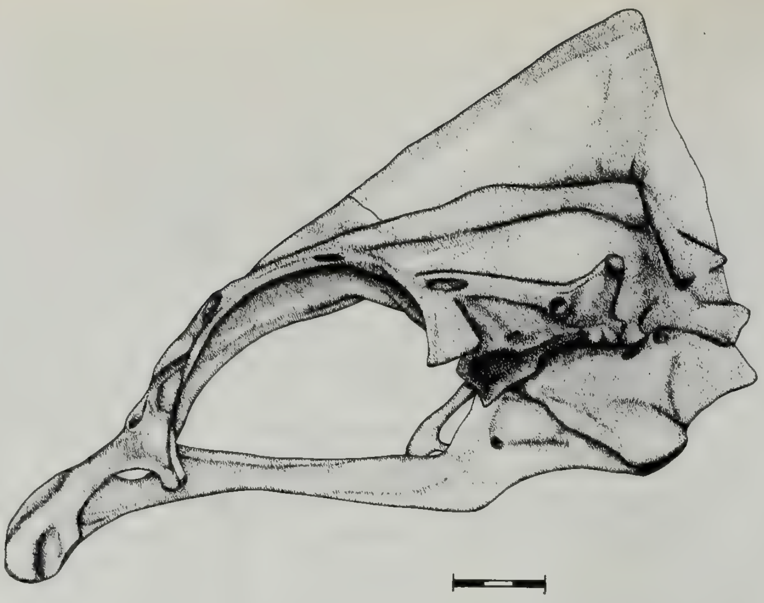

Fig. 8. *Pharyngochromis acuticeps*. Outline drawing of the neurocranium in left lateral view. Scale: 3 mm. Drawn by Elaine Grant.

In adult males the scale centres on the flanks and upper two-thirds or more of the caudal peduncle are deep maroon; in breeding livery this colour extends to the scale edge, giving a purplish sheen to the upper part of the body. Such fishes have brightly iridescent blue-green (almost turquoise) lips and the branchiostegal membrane is dusky. Jubb (1967), presumably describing Zambezi or Save-Runde fishes, records that the forehead in breeding males assumes a claret colour.

Depending on the emotional state of the individual, the body and caudal peduncle are crossed, at least over their dorsal three-quarters or half, by 8 to 10 dusky bars, often with the upper halves of one or two bars approaching and virtually fusing with one another ventrally. In this way the otherwise well-spaced and regular barred pattern is broken by near V-shaped marks. An interrupted and horizontal dusky stripe is often present, running mid-laterally along the body from immediately behind the operculum to the caudal fin origin where it expands slightly to form a rounded terminal spot. A dark lachrymal stripe passing through the eye and onto the dorsum is sometimes present, and is continued ventrally behind the posterior tip of the maxilla.

The dorsal fin membrane is light greenish-grey, the lappets and margin of the soft fin are bright orange. Immediately below the orange there is a thin white band, particularly noticeable on the spinous part of the fin. Below this band there is a wider and more diffuse band of dark green-grey to charcoal pigment which is also most intense over the spiny part of the fin. The entire or greater part of the dorsal fin membrane carries rust-red to brownish-orange spots. These are most clearly defined and numerous on the soft part of the fin, whereas on the spinous part the spots generally coalesce into streaks or blotches. These markings are most intense in sexually active males.

The pelvic fins are hyaline to very pale lemon-yellow, but with the membrane between the spine and the first two branched rays dusky in adult males; in sexually active males the whole fin is black or dusky.

The caudal fin is hyaline to pale yellow, often with a slightly dusky margin, especially posteriorly, and with numerous very dark orange or red, near rusty spots over its proximal half. These spots, like those on the dorsal fin, intensify in breeding males.

The pectoral fins are hyaline.

The anal fin is hyaline with a rosy-pink margin in adult males. Both sexes have orange spotted anal fins, but the spots are brighter, larger and more numerous in adult males. There is extensive intraspecific variability in the number and size of the spots, especially in males, but none is ever a true ocellus; that is, the central coloured area is not surrounded by a concentric and transparent band (see Greenwood, 1979: 275).

Judging from the live and recently preserved material I have examined, the coloured centre of each spot, at least in adult males, is usually circumscribed by a very narrow, dark margin. It also seems likely that the margin is only present in adult males, but this observation requires confirmation.

As noted previously, the number and arrangement of anal spots in *P. acuticeps* is variable, with the number ranging from as many as eighteen small spots irregularly dispersed over the entire fin, to as few as three or four large spots in a roughly triangular configuration (*cf.* plate 46 in Jubb, 1967, with fig. 151 in Poll, 1967). Other combinations are not uncommon; for example, amongst Okavango fishes there can be up to ten spots arranged in two approximately horizontal and parallel rows, a similar number of spots aligned in three roughly parallel and posteroventrally sloping rows, or a basically neat and linear pattern but with some randomly distributed spots as well.

From the fresh and preserved material examined, it was not possible to establish any clear-cut correlation between geographical locality and the type or pattern of spots present. Few, that is two or three, and large spots were not found amongst fishes from the Okavango region, and numerous, small irregularly arranged spots were not recorded from the small sample of Angolan fishes available (see p. 48, Discussion).

There is some indication that, in the Okavango and several Zambezian populations, the number of spots may increase with the size of the individual, and that the spots are less obvious in small fishes. However, in the three males from Lake Calundo, Angola, which I examined, there are only three spots in individuals of a size (57.0–71.0 mm S.L.) at which there would be many more in specimens from the Okavango system. But, the spots in the Lake Calundo fishes were much larger than those seen in any Okavango specimens, and thus, in terms of their value as signals to the female, may be of equivalent effectiveness to the more numerous markings in the Okavango fishes (see Hert, 1989, for a discussion on the function of anal markings in mouth-brooding cichlids).

The coloration of preserved material. The ground colour of the body shades from greyish-brown dorsally to fawn ventrally, and is darkest on the dorsum of the head. The darkly pigmented scale centres are obvious as, in most specimens, are the vertical and horizontal markings on the flanks and caudal peduncle (see p. 46), and the lachrymal stripe with its narrow posterior continuation running behind the posterior tip of the maxilla.

Fin maculations (including the anal fin spots) are dark brown, the narrow black margin to the anal spots usually visible under low magnification. In long-preserved specimens, especially those fixed and kept in alcohol, the anal fin markings are difficult to detect, as are the maculations on the other unpaired fins.

In adult males the pelvic fins are dusky, the extent of the pigmentation depending on the fish's level of sexual activity (see above).

The lappets of the spinous dorsal fin, and the margin of its soft part are colourless and thus become continuous in preserved specimens with the area of the underlying white band visible only in live or fresh specimens.

BIOLOGY

Apart from detailed papers by Balon & Muyanga (1974) and Hustler & Marshall (1990) on respectively age and growth, and population dynamics of *P. acuticeps* in Lake Kariba only generalized accounts of the species' biology are available, and then mainly for fishes also from the Zambezi system (Jackson, 1961; Kenmuir, 1983; Bell-Cross & Minshull, 1988). These accounts, supplemented by personal observations on fishes in the Okavango system, indicate that *P. acuticeps* is a highly eurytopic species, inhabiting fast and slow flowing waters as well as open lagoons, small dams and other artificial impoundments, including the rocky shore-line of Lake Kariba.

Trophically *P. acuticeps* is an omnivorous carnivore which includes small fishes as well as insects and crustaceans in its diet.

Little is on record about the species' reproductive biology except that it is a female mouth-brooder and that the male makes a small sandscrape nest in shallow water (Jubb, 1952; Bell-Cross & Minshull, 1988). Judging from the Okavango material examined, females are sexually mature at a standard length of about 60 mm, and males at about 65 mm.

DISTRIBUTION

Pharyngochromis acuticeps, in its various synonymic guises, has been recorded from the Zambezi system in Zambia and Zimbabwe; the Save-Runde system, the Okavango river and its delta swamp system; Lake Calundo, a waterbody associated with an Angolan tributary (Luena river) of the upper Zambezi; from an unknown locality in Angola (the types of the species) and, also in Angola, from the Lucala river, a northern tributary of the Quanza river (Boulenger, 1915; Barnard, 1948a; Jackson, 1961; Poll, 1967; Jubb, 1967; Jubb & Gaigher, 1971; Skelton *et al.*, 1955; Bell-Cross & Minshull, 1988).

Jubb's (12967: 47 & 171) record of the species (as *Haplochromis darlingi*) from the Limpopo river, repeated by Greenwood (1979: 311), is probably a *lapsus*. I have been unable to locate material from that source in any of the museums with which Jubb was associated, and neither has any material been collected from the Limpopo system in recent years. Doubt is also cast on Jubb's Limpopo record by Bell-Cross & Minshull (1988), who note that the presence of the species '. . . south of the Zambezi on the East Coast needs confirmation'.

Pharyngochromis acuticeps has been recorded (as *Pelmatochromis welwitschi*) from the Kuso river, Cunene drainage, Angola, by Pellegrin (1936). Poll (1967: 313), who considered Pellegrin's material to be misidentified *Haplochromis darlingi*, accepted this record. However, there is no indication that he examined Pellegrin's specimens, and I have been unable to locate them. Since no further material of *Pharyngochromis acuticeps* has been collected from the Cunene river (Greenwood, 1984; Bell-Cross & Minshull, 1988), and until it is possible to examine Pellegrin's fishes, the presence of the species in that system should be considered as uncertain but not improbable (see Bowmaker *et al.*, 1978: 1194–9, and fig. 8).

REVISED GENERIC DIAGNOSIS FOR *PHARYNGOCHROMIS*

Information derived from the large number of specimens now available, and the consequent knowledge of intrageneric variability, requires some modification to the original diagnosis and description (Greenwood, 1979: 310–311; 316), *viz*.:

Body depth: variable, from 27 to 41% of standard length.
Cheek: with 4–6 (rarely 3) horizontal rows of scales.
Squamation: Lateral-line with 31–36 scales (modal range 32–34), the last 5–7 (rarely 4 or 8) pored scales of the upper lateral-line separated from the dorsal fin base by one large and one small scale; 15, rarely 16 scales around the caudal peduncle.
Dorsal fin: with 14–16 (mode 15) spinous and 11–13 (mode 12), rarely 10 or 14, branched rays. Anal fin with 3 spinous and 8 or 9 (no distinct mode) branched rays.
Anal fin spots: variable in number (from 3 or 4 large to 18 small spots) and in arrangement (from regular and linear to irregularly scattered). Vertebrae (excluding the urostylar centrum): 28–31, comprising 13 (rare) to 16 (rare), modally 14, abdominal and 14–16 (mode 15) caudal elements.

Other features in the original description of the genus remain unaltered.

DISCUSSION

The discussion includes comments on the generic placement of *Chetia brevis* Jubb, 1968, and the status of that genus.

On an intracontinental scale, *Pharyngochromis acuticeps*, as here construed, has a wide and disjunct distribution, essentially one involving the Okavango, Zambezi and Quanza river systems. Even within one of those extensive systems, the Zambezi, there is a major barrier to dispersion, the Victoria Falls, and there could well be other unrecognised physical or biotic barriers in each system.

As with many other allopatrically distributed cichlid species, the *P. acuticeps* pattern raises questions concerning the conspecific status of the various geographically circumscribed elements involved. In past geological periods the major river systems, or their forerunners, in which *P. acuticeps* occurs have been interconnected (Bowmaker *et al.*, 1978), and their contemporary fish faunas seem to share a number of species (Poll, 1967; Jubb, 1967; Jubb & Gaigher, 1971; Bowmaker *et al.*, 1978; Greenwood, 1984; Skelton *et al.*, 1985). Those shared elements, which in effect are morpho-species, are assumed to be conspecific, but they could also be aggregates of vicariant sibling sister-species whose status has not been recognised. In part, this problem stems from a lack of biological information (especially ethological data), in part from the particular species concept employed by the workers concerned, and partly from a reticence to burden the literature with specific names for taxa supposedly, and perhaps even truly indistinguishable on morphological grounds. It is against that background that I would consider the seemingly monotypic status of *Pharyngochromis*.

If one takes into account the present physical separation, and thus effective extrinsic reproductive isolation between populations (*sensu lato*) of *P. acuticeps* living above and below the Victoria Falls, and the physical separation of the populations (again *sensu lato*) inhabiting the Zambezi, Okavango and Quanza systems, then these could well meet the requirements of the evolutionary species concept. That is, a lineage of ancestor-descendent populations reproductively isolated from other such lineages, and with its own evolutionary tendencies and historical fate (see various discussions of this concept in Otte and Endler, 1989).

The evolutionary species concept could also be applied at a lower level of geographical isolation if, for example, different populations within a single river system were reproductively isolated from one another by some ecological or abiotic factor.

For the moment, however, there are insufficient data available for *P. acuticeps* to establish, on the grounds of extrinsic reproductive isolation, whether or not the evolutionary species concept is applicable either to the populations occupying the three major areas of its distribution (see above) or to populations within a single river system.

Likewise, there are insufficient data to test the applicability of the phylogenetic species concept, *viz*. that a species is '. . . an irreducible (basal) cluster of organisms diagnosably distinct from other such clusters, and within which there is a parental pattern of ancestry and descent' (Cracraft, 1989).

Despite the extent of 'intraspecific' variability manifest by the *P. acuticeps* specimens described above, it has not proved possible to diagnose into irreducible clusters any particular group of specimens. The very unequal sizes of the samples from different localities is one difficulty here, as is the absence of detailed information on the coloration of sexually active males from the various localities. Since male coloration in mouth-brooding haplochromine cichlids is likely to be an important component of a species specific mate recognition system, *sensu* Paterson, 1985 (see Greenwood, 1974; 1981; 1991), that omission is a serious one. So, too, is the lack of detailed information on possible population or geographical differences in the size, pattern and colours of anal fin spots in males, or possibly even in both sexes (see p. 47). In addition to their use for defining a phylogenetic species, such data would be essential if the 'Recognition' species concept of Paterson (1985) were to be utilized, *viz*. a species is the most inclusive population of individual organisms with a common fertilization system.

At one point in this study it seemed possible that the pattern and size of anal spots (see p. 47) could have some geographical correlation, but the range of variation in samples from the Okavango swamps, even within a single locality, seriously weakens that possibility. Nevertheless, the combination of few and large spots seen in males from the small sample of Lake Calundo fishes (p. 47) is apparently unique, but the sample is too small to warrant its recognition, and naming, as a phylogenetic species on that basis alone.

Other seemingly diagnosable assemblages are provided by the samples from Kazungula, near the Victoria Falls (Zambezi system), and from the Popa rapids on the Okavango river. When compared with others from elsewhere in either river system, specimens from these localities have very small and sometimes deeply embedded scales laterally on the thoracic region. However, in both localities the water is fast-flowing and turbulent, and the substratum is composed mainly of large stones and rocks. Reduced and embedded thoracic scales are often (Trewavas, 1983), but not invariably (Greenwood, 1979) associated with such habitats. Thus, the thoracic squamation in these *P. acuticeps* populations may well be an ecophenotypic response to a rocky and turbulent habitat. Even if the character is genetically fixed, it could be an example of intraspecific parallelism in response to similar environments, and not an indication of the two populations being conspecific and distinct from other *P. acuticeps*. To establish the latter case would require the recognition of congruent synapomorphies uniquely shared by the two rapid-water populations. But, as with all other and physically isolated populations of *P. acuticeps*, none was detected.

Clearly a lot more information, both morphological and ethological, is needed before the present morpho-species *P. acuticeps* can be seen in its true biological perspective.

Perhaps the most realistic phylogenetic interpretation of this situation is to consider the current morpho-species an aggregate of at least five evolutionary species, namely the populations living above and below the Victoria falls in the Zambezi system, populations in the Quanza river (Angola) and those in the Save-Runde and in the Okavango systems. Unfortunately there is no satisfactory way to express that conclusion within the existing system and rules of formal taxonomic nomenclature. To use the category of subspecies is to contradict the evolutionary species concept, and at present it is impossible to provide diagnostic features for the five groups, other than their geographical circumscription, and thus formally establish them as phylogenetic species.

The phyletic interrelationships of *P. acuticeps*, be it a monotypic or a polytypic genus, have not been established more firmly by the additional data now available. The situation remains essentially the unsatisfactory one discussed in my earlier paper (Greenwood, 1979: 312), where interrelationships within the supposed lineage *Pharyngochromis, Chetia* and *Serranochromis* were considered.

Within that lineage, and as compared with *Serranochromis*, both *Chetia* and *Pharyngochromis* share the plesiomorphic condition of lower numbers of abdominal vertebrae, but *Pharyngochromis*, unlike *Chetia* and *Serranochromis*, has the apparently apomorphic condition of more than the last two or three pored scales of the upper lateral-line being separated from the dorsal fin base by only one large and one small scale (Greenwood, 1979: 271).

The genus *Chetia* has, since my 1979 paper, been enlarged by the addition of two species, *C. mola* of Balon & Stewart (1983) from the Zaire system, and the referral to it (Greenwood, 1984) of *Pelmatochromis welwitschi* Blgr (1898) from Angola. Also, I would now revise my earlier view (Greenwood, 1979: 307) that *Chetia brevis* Jubb (1968) should be excluded from the genus. That earlier opinion was based partly on Jubb's description of the anal markings in *C. brevis* as a few large, ocellate spots, and in part on the fact that bicuspid outer jaw teeth are present in specimens of 86–89 mm standard length, a size at which only unicuspid teeth are present in the type specimens of the type species, *C. flaviventris* Trewavas (1961).

Recently I examined the holotype and additional specimens of *C. brevis* (housed in the Albany Museum) as well as colour transparencies of live fishes, and find that the anal spots are not ocellate, and are quite unlike the true ocelli in many haplochromine species (Greenwood, 1979: 274–5). Granted, the spots in *C. brevis* are larger, and fewer, than those in *C. flaviventris*, but judging from the situation in *Pharyngochromis acuticeps* (see p. 47) such variability can occur intragenerically and, if the latter taxon is truly monotypic, intraspecifically as well.

With regard to the dental morphology of *C. brevis*, further material of *C. flaviventris*, from the Limpopo system, shows that, unlike the situation represented in the type series, bicuspid teeth can persist in fishes up to a standard length of 80 mm.

Thus, there are no reasons for excluding *C. brevis* from *Chetia*, or, when its various anatomical and morphological characters are taken into account (see Jubb, 1968), for considering it conspecific with *C. flaviventris*.

Chetia welwitschi, known only from its holotype and two other specimens, all from Angola, appears to be more similar to *C. ventralis* than to *C. brevis*, and is readily distinguishable from *C. mola* whose massive pharyngeal jaws and dentition are unique within the genus (Balon & Stewart, 1983; Greenwood, 1984). Indeed, in its hypertrophied pharyngeal jaws *C. mola* approaches the conditions seen in several *Serranochromis (Sargochromis)* species and exceeds those in others such as *S. (S.) greenwoodi* and *S. (S.) gracilis*. However, there is seemingly no reason for placing the taxon in that genus and subgenus (Balon & Stewart 1983), and in the present state of our knowledge about the fluviatile haplochromines, its place would seem to be in the genus *Chetia*.

The existence in *Chetia* of anatomical and dental specializations associated with mollusc eating (*C. mola*) and piscivory (*C. flaviventris* and possibly *C. welwitschi*), and similar specializations occurring in each subgenus of *Serranochromis*, raises interesting, but for the moment untestable speculations about the phyletic relationships of the three taxa.

The problem is complicated by the fact that both subgenera of *Serranochromis* share the apomorphy of increased numbers of abdominal vertebrae (Greenwood, 1979), but there is no currently identified synapomorphy uniquely shared by *Chetia* and *Serranochromis*.

Indeed, as presently construed, there is no autapomorphic feature characterizing *Chetia*. Previously, when that taxon was monotypic, the supposedly early appearance of an entirely unicuspid jaw dentition, and possibly the reduced number of inner tooth rows in both jaws, were considered as generic autapomorphies (Greenwood, 1979). With the inclusion of at least *C. brevis*, the early appearance of a unicuspid dentition can no longer retain its status as a generic apomorphy, a loss which, anyway, would follow from the discovery of the relatively delayed appearance of such teeth in other populations of *C. flaviventris* (pers. obs. on Limpopo specimens in the RUSI and AMG collections). Since only large specimens of *C. mola* and *C. welwitschi* are known (Greenwood, 1984) growth related changes in their oral dentition cannot be checked. All four *Chetia* species do, however, show a reduction in the number of inner tooth rows in both jaws, but the polarity of that character is difficult to ascertain.

In other words, in a phylogenetic context it seems that *Chetia* could be a catch-all category for those fluviatile haplochromines with non-ocellate and multimaculate (or sparsely spotted) anal fins, but which do not have the apomorphies characterizing *Serranochromis* (increased number of abdominal vertebrae) or *Pharyngochromis* (the increased number of posterior upper lateral-line scales separated from the dorsal fin base by one large and one small scale).

The reality of *Pharyngochromis* as a distinct and monophyletic lineage within the supposed *Serranochromis—Chetia* phyletic assemblage (Greenwood, 1979) rests for the moment on the lateral-line scale character combined with the absence of other derived features shared uniquely with either *Serranochromis* or any species of *Chetia*. An unsatisfying and unsatisfactory situation, but one frequently encountered within the Cichlidae. In my view, the situation would not be improved by placing *Pharyngochromis* in the currently indefinable genus *Chetia*, with one of whose species (*C. brevis*) *P. acuticeps* bears a superficial resemblance (Jubb, 1968), but does not share the lateral-line/dorsal fin base scale character.

Interestingly, but at present inexplicably, no *Chetia* species coexists with *Pharyngochromis acuticeps* or, indeed, even occurs within the same drainage system. In contrast, there is complete distributional overlap, except in the Save-Runde system, between the *Serranochromis* subgenera and *Chetia*, as well as an overlap between *Serranochromis* and *Pharyngochormis acuticeps* (Bell-Cross & Minshull, 1989); only *P. acuticeps*, however, occurs in the Save-Runde system.

Appendix

The principal morphometric and meristic features of material from the Zambezi and Okavango systems, the somewhat atypical Zambezian population (see p. 49) from Kazungula near the Victoria Falls, (Table 1), and of the type specimens examined (Table 2).

Abbreviations and symbols used in these tables are:

+:	Expressed as a percentage of standard length
*:	Expressed as a percentage of head length
A:	Anal fin formula
Cp:	Caudal peduncle length
Cp l/d:	Length-depth ratio of caudal peduncle
D:	Dorsal fin formula
Gr:	Outer gill-rakers on the first ceratobranchial
Interorb:	Least interorbital width
Preorb:	Depth of preorbital (ie. lachrymal bone)
Ll. scales:	Scales in the lateral series

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Table 1

	Zambezi system Excluding Kazungula specimens n = 28 Size range 32.5–133.0mm SL		Okavango system n = 58 Size range 27.5–102.0mm SL		Kazungula (Zambezi system) n = 5 Size range 53.0–75.0mm SL	
		M		M		M
Depth^{+}	27.6–35.7	34.3	30.8–40.6	35.5	30.2–35.7	32.4
Head^{+}	30.7–36.9	33.7	31.0–37.7	33.8	34.7–36.7	35.9
Preorb.*	14.7–25.6	19.6	14.3–24.2	20.5	15.8–20.8	18.5
Interorb.*	15.0–25.6	19.5	14.3–22.9	19.9	15.4–20.8	17.7
Snout*	28.0–37.2	32.2	25.0–36.7	32.2	31.6–35.6	33.5
Eye*						
<80.0 mm S.L. (n=20)	27.3–36.0	30.9	<70.0 mm S.L.(n=31) 28.0–36.4	31.8	29.2–31.6	29.6
>80.0 mm (n=8)	22.2–29.3	25.6	>70.0 mm S.L. (n=27) 25.4–21.3	28.3		
Cheek*	16.0–31.4	23.9	17.6–27.0	24.7	20.5–22.9	21.5
Lower jaw*	34.8–48.9	41.2	35.7–43.6	39.7	37.5–40.0	38.4
Cp.$^{+}$	15.9–21.0	17.9	15.4–21.8	17.6	16.9–19.5	18.1
Cp.l/d	1.2–1.7 Mode 1.5–1.6		1.2–1.8 Mode 1.5–1.7		1.4–1.8	
D.	XIV or XV (Mode XV)		XIV–XVI (Mode XV)		XIV or XV	
	10–12 (Modes 11 & 13)		11–14 (Mode 12)		11 or 12	
A.	III 8 or 9 (Mode 8)		III 7–10 (Mode 8)		III 8	
Ll.sc.	30–34 (Modes 32 & 33)		31–35 (Mode 33)		32–34	
Cheek scales	4–6 (Modes 4 & 5)		4–5 (Mode 4)		3 or 4	
Gr.	7–10 (Mode 9)		7–12 (Mode 10)		8 or 9	

Table 2

	Chromis jallae	*Pelmatochromis darlingi*	*Pelmatochromis multiocellatus*	*Chromis acuticeps*	
	Holotype, 59.0mm SL	Holotype, 84.5mm SL	Holotype, 97.0mm SL	Lectotype, 59.5mm SL	Paralectotype, 68.0mm SL
Depth$^+$	28.8	34.3	34.0	32.0	32.4
Head$^+$	30.5	34.3	35.9	37.0	37.5
Preorb.*	22.2	20.7	18.6	15.9	15.7
Interorb.*	16.6	20.7	20.1	20.5	20.8
Snout*	33.3	33.7	33.1	29.5	33.3
Eye*	27.8	29.3	25.9	27.3	27.5
Cheek*	25.0	27.5	24.4	22.7	23.5
Lower Jaw*	36.1	41.4	43.1	40.9	43.1
Cp.$^+$	21.8	17.5	15.5	18.5	17.6
Cp. l/d	1.8	1.4	1.2	1.6	1.5
D.	XV, 10	XV, 11	XVI, 10	XV, 11	XV, 11
A.	III, 8	III, 8	III, 9	III, 9	III, 9
Ll.sc.	32	*ca.*30	32	31	*ca.*32
Ck.sc.	6	5	5	4	5
Gr.	8	10	9	10	9

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Description of a new species of *Microgale* (Insectivora: Tenrecidae) from eastern Madagascar

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SYNOPSIS. A new species of *Microgale* (shrew-tenrec) from primary forest in eastern Madagascar is described. Morphological comparisons are made with other members of the genus, in particular with those of the *Microgale cowani* and *M. gracilis* clusters, with which it shows greatest affinity.

INTRODUCTION

Eleven species of shrew-tenrecs belonging to the genus *Microgale* are currently accepted (MacPhee, 1987; Jenkins, 1988). The genus was believed to be much more diverse until the revision by MacPhee (1987) showed that over half of the named forms of *Microgale* were merely juveniles or morphological variants. Fortunately in the present case, adults of both sexes, a subadult and a juvenile were included in the small sample collected, so that adults could be distinguished with a good measure of confidence from those of other species and some observations were possible on the deciduous dentition. Distinctive cranial and dental features characterise the new species, which is further distinguished from most other species by its large size.

Brief comments are included on the other species of *Microgale* collected from the same locality.

MATERIALS AND METHODS

Small mammal trapping was carried out for two months by the Madagascar Environmental Research Group in primary forest of the Ambatovaky Forest Reserve (Barden, in prep.). A mixed collection of rodents and small tenrecs was collected, including the undescribed form. Preliminary identifications based on external features were made by members of the Research Group, who then brought the specimens to The Natural History Museum [BM(NH)] for formal identification, which in these mammals, requires the examination of a suite of craniodental characters in addition to external features. The preliminary identifications were recorded (Nicoll & Rathbun, 1990), some of which were found to be incorrect following detailed examination.

Measurements were taken with dial calipers and are given in millimetres. The dental nomenclature follows that of Mills (1966), Swindler (1976), Butler & Greenwood (1979) and MacPhee (1987). The following abbreviations are used in the text c.—circa, GCL—greatest cranial length, HB—head and body length.

Microgale dryas sp. nov.

HOLOTYPE. BM(NH)91.230, collector's number RAN 33610, adult female, in alcohol, skull extracted. Collected 20 February 1990 by Tanya Barden and Christopher Raxworthy, Madagascar Environmental Research Group from Site 1, Ambatovaky Special Reserve, [northeast] Madagascar, 16°51'S 49°08'E, in primary rainforest, between 600–750 metres altitude.

Paratypes: BM(NH) 91.227, collector's number RAN 33592, adult male; BM(NH)91.228, collector's number RAN 33593, juvenile female; BM(NH)91.229, collector's number RAN 33596 subadult male. All with the same collection data as the holotype but collected 14 February 1990.

RESULTS

Diagnosis

Intermediate in size between the smaller *M. thomasi* Major, 1896 and *M. gracilis* (Major, 1896), and the larger *M. dobsoni* Thomas, 1884 and *M. talazaci* Major, 1896. Braincase narrow relative to skull length. Upper second and third premolars (P^3 and P^4) with well defined anterior ectostyle, separated by a notch from the distinct posterior ectostyle and distostyle. Mid region of guard hairs of the dorsal pelage flattened and broadened in cross-section.

Description

Size large; external measurements follow with those of the holotype in brackets: head and body length 105.5–113.5 (105.5), mean 110.9, SD 3.16; tail length 68.0–70.5 (70.4), mean 69.5, SD 1.02; hindfoot length 18.1–18.7 (18.7), mean 18.5, SD 0.23; weight 38–40 grams (38), mean 39.25, SD 0.83. Tail greater than half as long as head and body length: 60–67% (67%), mean 62.8%, SD 2.68. Dorsal pelage dark reddish or greyish brown, with a grizzled appearance; bases of hairs grey, distal portion light brown or red brown, some with black tips; interspersed with long guard hairs which are grey at the base but black for most of their length; unlike any other member of the genus, these hairs are flattened and broadened in cross-section in their mid portion, rounded in cross-section distally. Hairs of ventral pelage grey at the base with light grey tips; colour of dorsal pelage merges gradually with that of the venter. Forefeet grey brown dorsally, light ventrally; hindfeet grey brown above and below; tail uniformly grey. The claws of the forefoot are elongated; claws of the third digit of the hindfoot are 65.1–78.9% (65.1%), mean 71.28, SD 5.63 of the length of those of the forefoot.

The skull is long and gracile (see Figs 1–3); the rostrum is elongated but moderately robust; the interorbital region is narrow and slightly concave in dorsal view; the braincase is long and deep, yet narrow; the squamosal region is not inflated and the superior articular facet is angular and clearly visible in dorsal view; the sinus canal forms a markedly peaked curve (see Fig. 3). The mandible is long, moderately robust, the corpus is sinuous in profile, with a moderately deep and broad coronoid process; the angle between the dorsal articular facet and the coronoid process is shallow; the mental foramen lies below the anterior portion of P_3.

The dentition is moderately robust and illustrated in Figures 4 to 7. Interproximal diastemata are present between all the upper incisors and canine, those on either side of the first upper premolar (P^2) are large. Posterior basal cusps (distostyles) are well defined on all three upper incisors, that on the first incisor (I^1) is robust and more than half the height of the principal cusp; anterior accessory cusps are scarcely evident on the upper incisors; the upper canine lacks an anterior accessory cusp and mesiolingual cusp, while the distostyle is small, slender and approximately one quarter of the height of the principal cusp; the first upper premolar (P^2) is robust, with well defined anterior and posterior basal cusps; the second upper premolar (P^3) has a slender paracone, the anterior ectostyle is well developed and separated by a notch from the posterior ectostyle and distostyle, the talon is moderately large and the lingual shelf well developed; the third upper premolar (P^4) is similar in structure to P^3 in buccal aspect but the paracone is more robust and the anterior ectostyle separated from the well defined posterior ectostyle and distostyle by an even more distinct notch, the talon is large with a small yet well defined cusp; the upper molars are similar to those of other members of the genus, but the talons of M^1 and M^2 are broad and deep, while that of M^3 is lingually extended. Small diastemata are present on either side of the third lower incisor (I_3), the lower canine (C) and the first lower premolar (P_2); a small anterior accessory cusp is present on the lower canine; the first lower premolar (P_2) is large, being only slightly smaller than the second lower premolar (P_3); the anterior and posterior accessory cusps of P_2 are well marked, the main cusp is 'anteroflexed' due to the short convex anterior slope and the longer, concave posterior slope; the paraconid is well developed on P_3 and the third lower premolar (P_4), and on the molars (M_1 to M_3); the anterior face of the protoconid of P_4 and all the molars is markedly convex.

Etymology

The name of this species is derived from the greek σρυας, dryad or wood nymph.

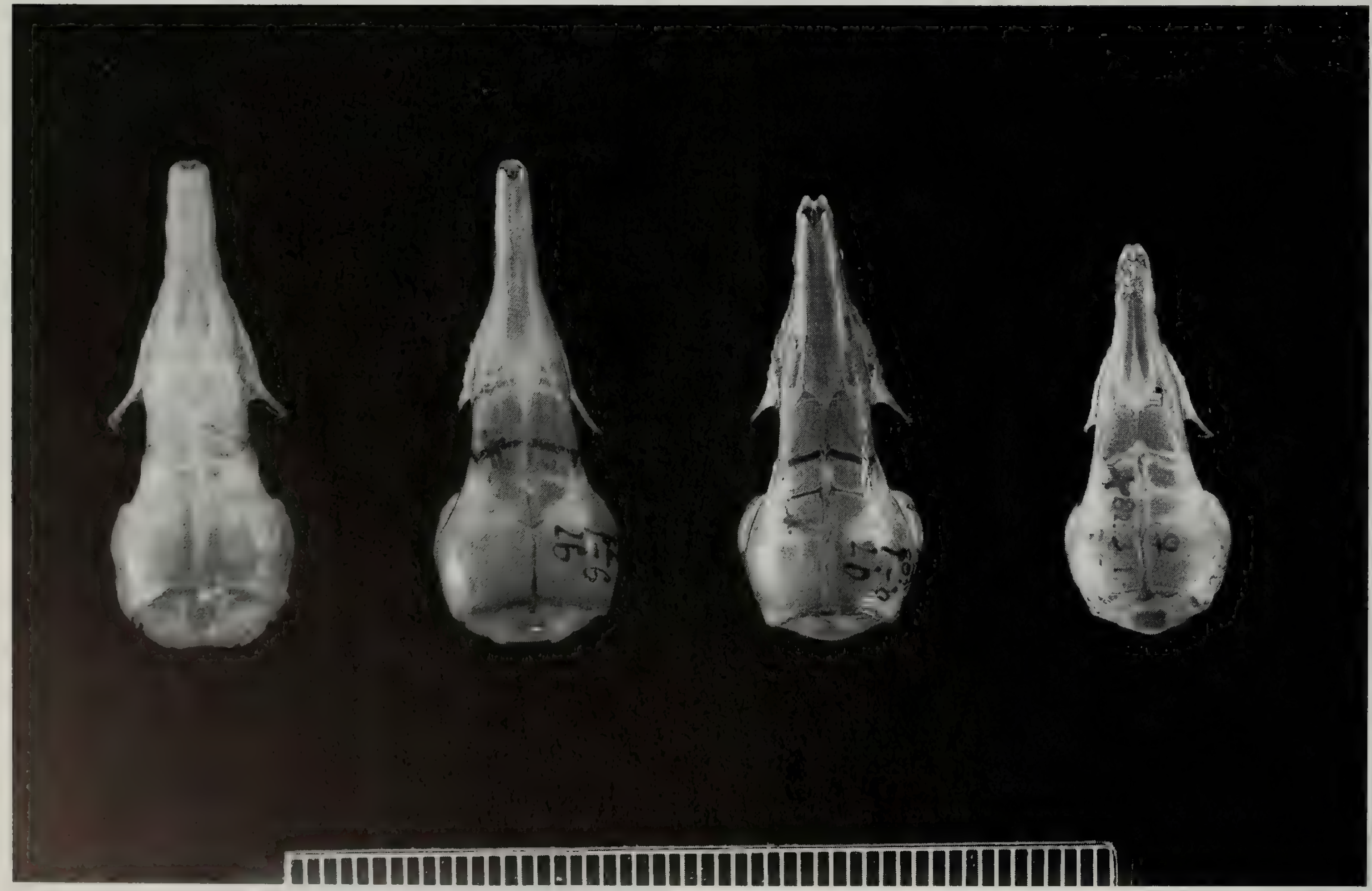

Fig. 1 Dorsal view of skulls, from left to right *Microgale dryas*, *M. gracilis*, *M. thomasi* and *M. cowani*. Scale 500 mm.

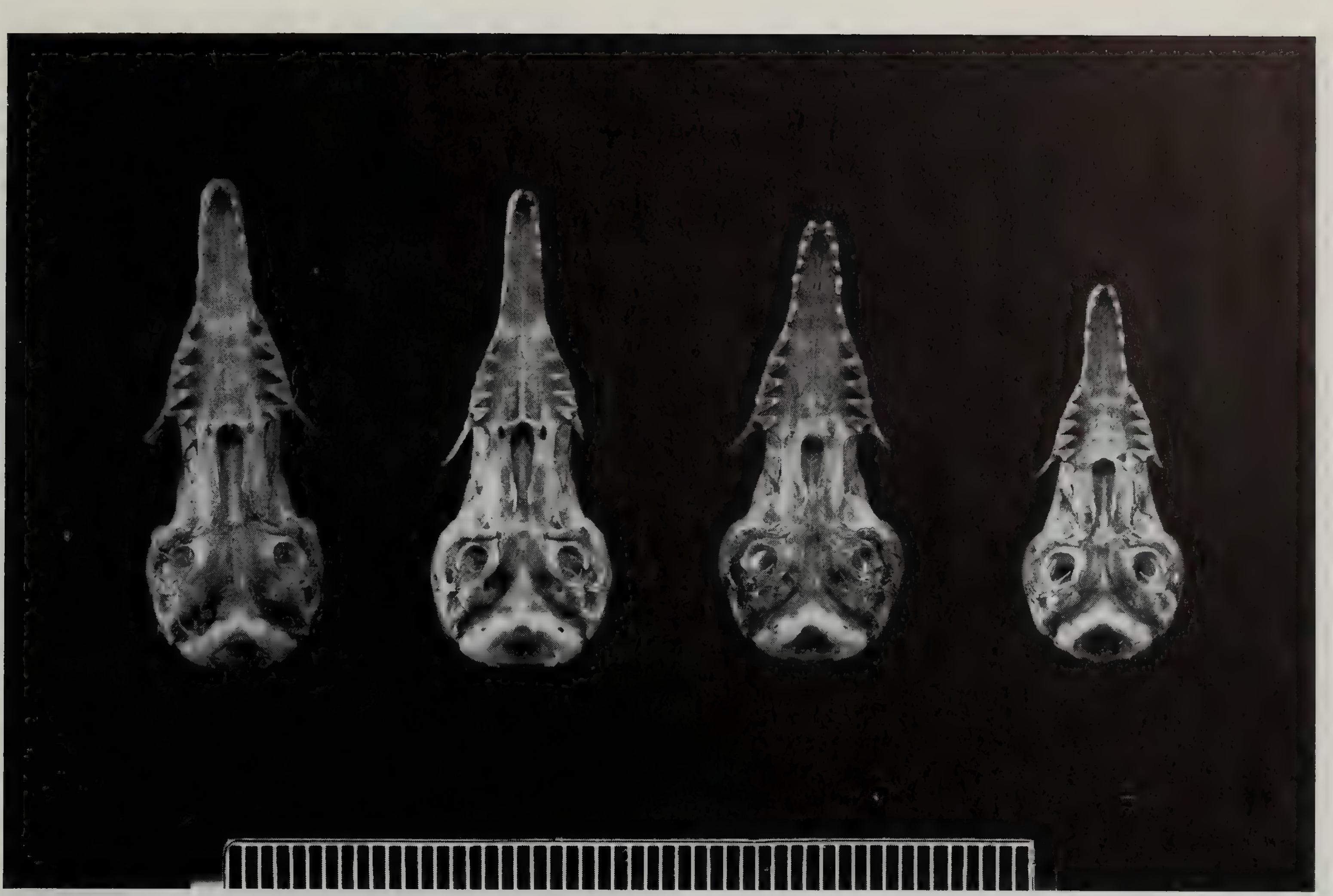

Fig. 2 Ventral view of skulls, from left to right *Microgale dryas*, *M. gracilis*, *M. thomasi* and *M. cowani*. Scale 500 mm.

Comparison with other species

Microgale dryas (HB 105–114, GCL 30–32) is intermediate in size between *Microgale thomasi* (HB < 98, GCL c.27) and *M. gracilis* (HB c.93, GCL c.29), and *M. dobsoni* (HB < 103, GCL > 29) and *M. talazaci* (HB > 115, GCL > 34). It is considerably larger than the other known species of *Microgale* (HB < 83, GCL < 25), see MacPhee (1987, table 2). It is readily distinguished from *M. talazaci* and *M. dobsoni* in which I_2 is larger than the lower canine, while, as in the other species of *Microgale*, I_2 is smaller or subequal to the lower canine.

M. dryas is distinguished from all other species by the dorsal pelage, in which the guard hairs are flattened and broadened in their mid region. On cranial and dental characters it is clearly associated with the *cowani* cluster [see MacPhee (1987), p.9], which includes *M. cowani* Thomas, 1882, *M. parvula* Grandidier, 1934, *M. pulla* Jenkins, 1988 and *M. thomasi*, and the *gracilis* cluster (*M. gracilis*).

All members of the *cowani* and *gracilis* clusters have gracile skulls with a long, narrow rostrum and diastemata between the anterior teeth. The skull of *M. dryas* is larger than any of the other members of the *cowani* or *gracilis* clusters and is intermediate in elongation of the rostrum between *M. thomasi* and *M. gracilis*. *M. gracilis* shows the greatest degree of attenuation of the rostrum, which is slender, with very long diastemata between the anterior teeth, in *M. dryas* the diastemata are moderately long (especially between the upper canine and P^2) and the rostrum is narrow (in these dimensions the new species resembles *M. cowani*) but in *M. thomasi* the diastemata are small and the rostrum is relatively broader and shorter (see Table 1). The interorbital region of *M. dryas* is narrow and slightly concave in dorsal view, in contrast to other members of the *cowani* and *gracilis* clusters in which the interorbital region increases in size from the anterior to the posterior region. The braincase of *M. dryas* is narrower relative to skull length than any of the other members of the genus; it is slightly narrower but deeper than that of *M. gracilis*, yet markedly narrower but deeper than that of *M. thomasi* (see Table 1). The squamosal region dorsal to the bulla is scarcely inflated in *M. dryas*, slightly inflated in *M. gracilis*, inflated in *M. cowani* and markedly inflated in *M. thomasi*; the sinus canal follows a shallow curve in *M. cowani*, *M. thomasi* and *M. gracilis* but forms a peaked curve in *M. dryas*. The corpus of the mandible of *M. dryas* is sinuous as in *M. cowani* and *M. gracilis*, unlike the straighter profile of *M. thomasi*; the mandible is shallower at the coronoid process in *M. dryas*, *M. cowani* and *M. gracilis*, than in *M. thomasi*.

Although only slightly larger than *M. gracilis* and with similarly elongated claws on the manus, *M. dryas* differs markedly from it in the cranial features given above and the following dental features. The toothrow length in *M. gracilis* is not markedly shorter than that of *M. dryas*, due to the much longer diastemata between the anterior teeth of *M. gracilis*, than those of *M. dryas*. The teeth of *M. gracilis* are smaller in all dimensions than those of *M. dryas* (buccal length x crown height of P_2 1.08 in *M. gracilis* but 1.64–1.85 in *M. dryas*). The most marked dental difference between the

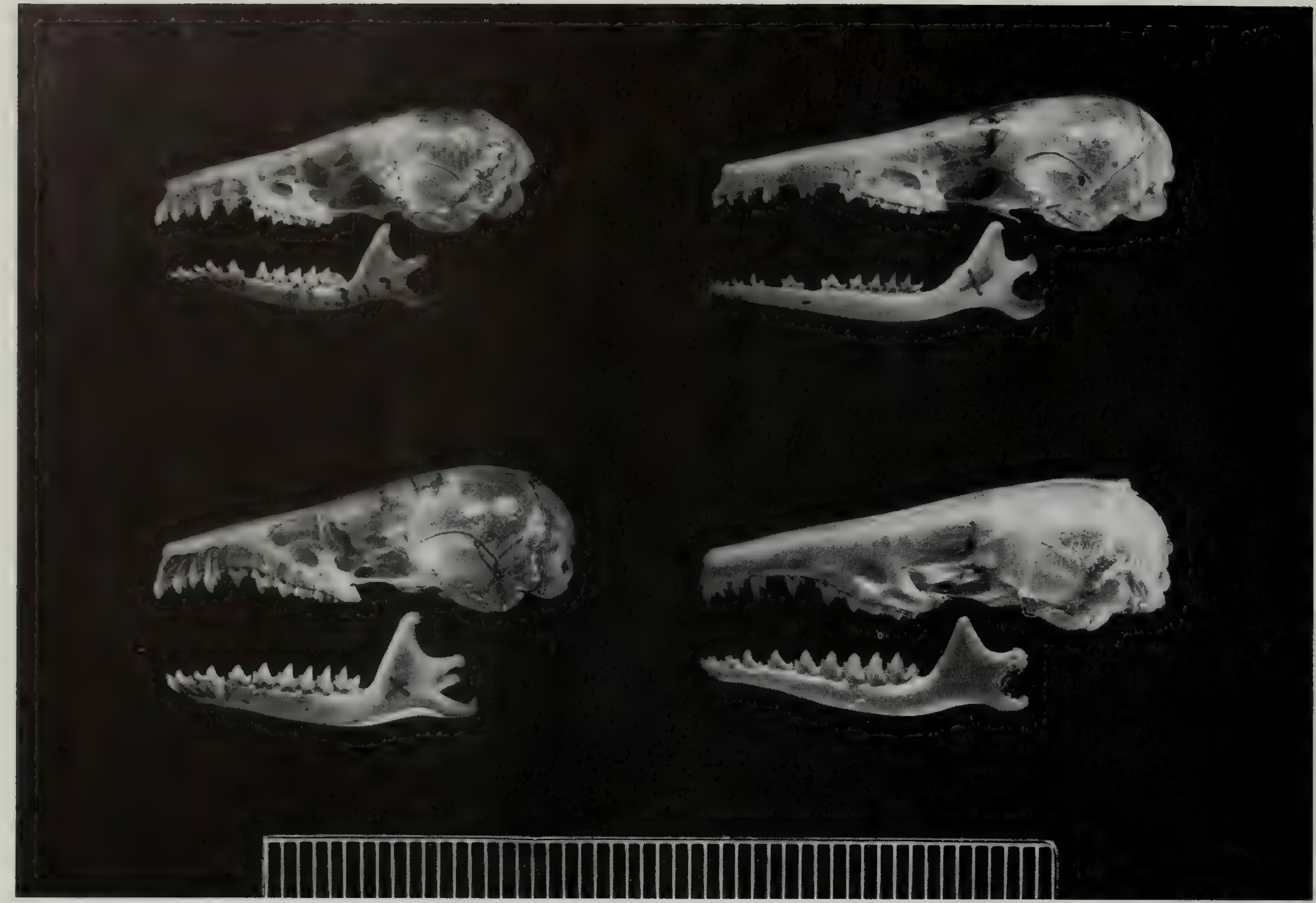

Fig. 3 Lateral view of skulls, top row left *Microgale cowani*, right *M. gracilis*, bottom row left *M. thomasi*, right *M. dryas*. Scale 500 mm.

M. dryas and *M. gracilis* is in the size of the talon of the molariform maxillary teeth; this is large in *M. dryas* but in *M. gracilis* is effectively absent and more reduced than in any other species.

Microgale dryas and *M. thomasi* differ in the following dental features. The distostyle of I^1 is more robust and greater than 50% of the height of the principal cusp in *M. dryas*, while it is more slender and less than 50% of the height of the principal cusp in *M. thomasi*. A mesiolingual accessory cusp is present on I^3 in *M. thomasi* but absent in *M. dryas*. A mesiolingual cusp is present and the distostyle is larger, more robust and approximately one third of the height of the principal cusp in *M. thomasi*, while in *M. dryas* the mesiolingual cusp is absent or reduced to a ridge and the distostyle is small, slender and approximately one quarter the height of the principal cusp. In *M. dryas* the anterior ectostyle of P^3 is well defined and separated from the distostyle, and the talon is large, unlike the condition in *M. thomasi* in which the anterior ectostyle is not separated and the talon is small. The posterior ectostyle and distostyle of P^4 are moderately well defined and separated from the anterior ectostyle by a notch, the talon is large with a well defined cusp in *M. dryas* but in *M. thomasi* there is no posterior ectostyle, the distostyle is barely evident and merges with the anterior ectostyle, and while the talon is moderately large it lacks a well defined cusp. A posterior ectostyle is present on M^1 and the talon is large and unicuspid or bicuspid in *M. dryas* but in *M. thomasi* there is no posterior ectostyle and the talon is medium sized and unicuspid. In all the molariform teeth the talon of *M. dryas* is larger than that of *M. thomasi*. There are fewer differences in the mandibular teeth of the two species. The incisors are similar but there are no diastemata between the incisors of *M. thomasi*, while in *M. dryas* a diastema is present between I_3 and the canine of all specimens and between I_2 and I_3 of three of the four specimens. An anterior accessory cusp is present on the canine in *M. dryas* but not in *M. thomasi*. Although P_2 is similar in both species, there is a slight difference in shape, in *M. dryas* the tooth is anteroflexed and tends to be caniniform, while in *M. thomasi* it is not anteroflexed and more molariform in appearance. P_2 and P^2 in both species are larger relative to the rest of the toothrow than in any other species (see Table 1). The molariform teeth (P_4 to M_3) are similar in the two species except that the anterior face of the paraconid of M_1 and M_2 is markedly convex in *M. dryas* but only slightly convex in *M. thomasi*.

DISCUSSION

Microgale is a taxonomically complex genus containing many named forms, over half of which were shown to be juveniles or morphological variants (MacPhee, 1987). In his revision, MacPhee demonstrated the high morphological within-species variation found in the genus, and described and

Table 1 Comparing *M. dryas, M. thomasi* and *M. gracilis*

	M. gracilis	*M. thomasi*	*M. dryas*
Condyloincisive length	29.0	25.9, 26.8	30.4–31.0
mean			30.63
SD			0.23
n			4
Upper toothrow length	14.4	12.5, 13.1	15.2–15.6
mean			15.43
SD			0.18
n			4
Length of anterior teeth (I^1—anterior of P^3)	8.4	6.6	7.5–8.0
mean			7.78
SD			0.18
n			4
Breadth of rostrum (P^2–P^2)	2.5	3.5, 3.6	3.5–3.6
mean			3.55
SD			0.05
n			4
Ratio of length of anterior teeth (I^1–P^3) to upper toothrow length	0.58	0.50, 0.53	0.49–0.52
mean			0.50
SD			1.13
n			4
Ratio of breadth of rostrum (P^2–P^2) to upper toothrow length	0.17	0.27, 0.28	0.22–0.24
mean			0.23
SD			0.47
n			4
Braincase breadth	11.3	11.4, 11.5	11.2–11.6
mean			11.4
SD			0.14
n			4
Braincase height	7.2	7.5, 7.6	7.9–8.2
mean			8.05
SD			0.11
n			4
Ratio of braincase breadth to condyloincisive length	0.39	0.43, 0.44	0.37–0.38
mean			0.37
SD			0.36
n			4
Ratio of braincase height to braincase breadth	0.64	0.66, 0.66	0.70–0.71
mean			0.71
SD			0.36
n			4
Ratio of mandible height at coronoid process to mandible length	0.27	0.33, 0.36	0.26–0.30
mean			0.28
SD			1.45
n			4
Buccal length x crown height of P_2	1.08	1.49	1.64–1.85
mean			1.74
SD			0.08
n			3
Head and body length	c.93	91, 97	105.5–113.5
mean			110.88
SD			3.16
n			4
Tail length	73–81[1]	62–70[1]	68–71
mean	78.0	67.2	69.53
SD	3.46	4.91	1.02
n	4	3	4
Ratio of tail to head and body length	0.73–0.87[1]	0.66–0.75[1]	0.60–0.67
mean	0.83	0.69	0.63
SD			0.03
n	4	3	4

Note: [1] data from MacPhee (1987)

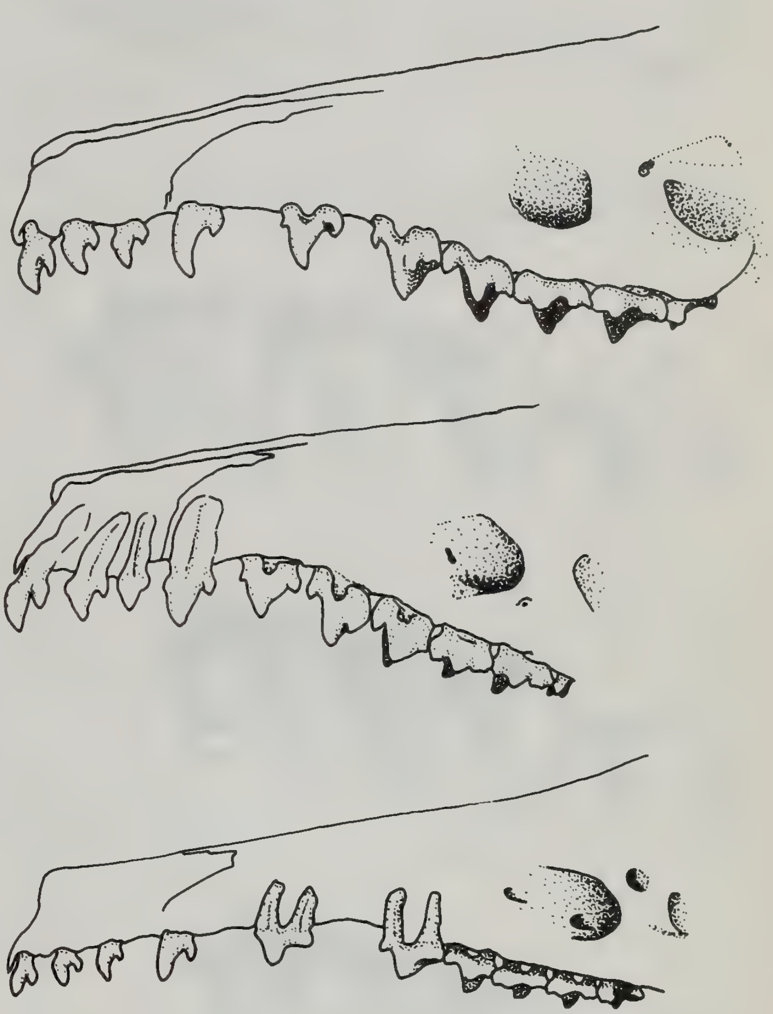

Fig. 4 Buccal view of left maxillary dentition of *Microgale dryas* (top), *M. thomasi* (middle), *M. gracilis* (bottom). Scale 1 mm.

illustrated the deciduous and adult dentitions of most species. Since the small sample of the new species contained a juvenile, subadult and two adults, it was possible to be confident that the specimens did indeed represent an undescribed species. MacPhee suggested the existence of growth curves, unusual in mammals, in which some subadults may exceed the average size of adults. This feature may be indicated by *M. dryas*, in which both the juvenile and subadult specimens are slightly larger than the adults in head and body length, although the small sample size precludes any meaningful comparison.

MacPhee divided the genus into six 'clusters' on the basis of dental traits and body proportions; he emphasised that this was a phenetic, not a phylogenetic arrangement. On the basis of the characters employed by MacPhee, *M. dryas* groups with the *cowani* and the *gracilis* clusters and is intermediate in many features between *M. thomasi* and *M. gracilis*. Since *M. thomasi*, *M. gracilis* and *M. dryas* are known from such small

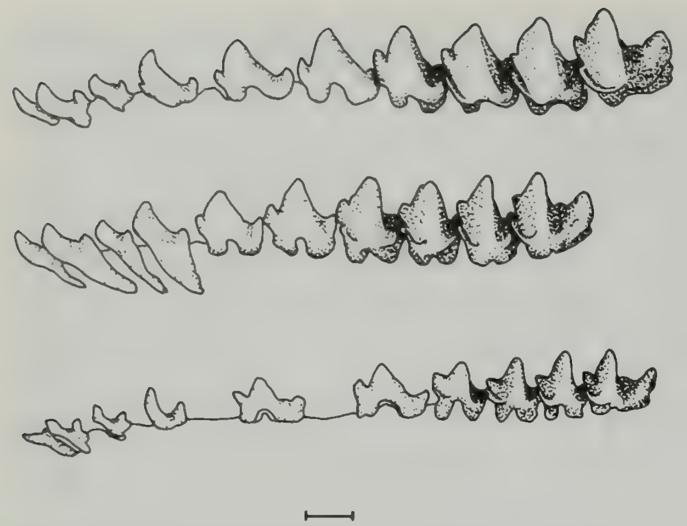

Fig. 5 Buccal view of left mandibular dentition of *Microgale dryas* (top), *M. thomasi* (middle), *M. gracilis* (bottom). Scale 1 mm.

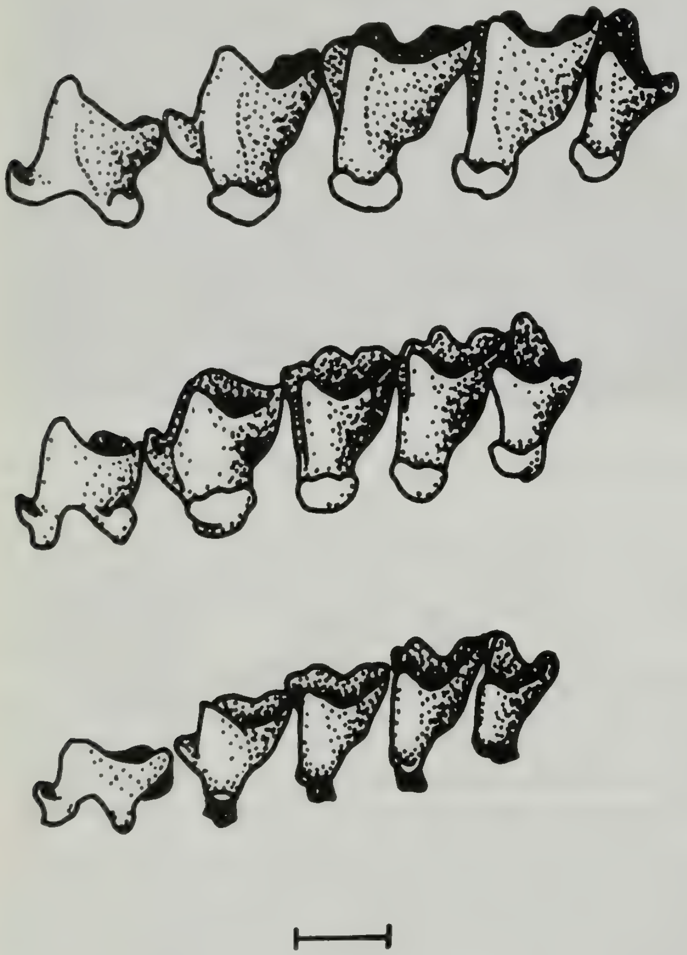

Fig. 6 Lingual view of left P^3 to M^3 of *Microgale dryas* (top), *M. thomasi* (middle) and *M. gracilis* (bottom). Scale 1 mm.

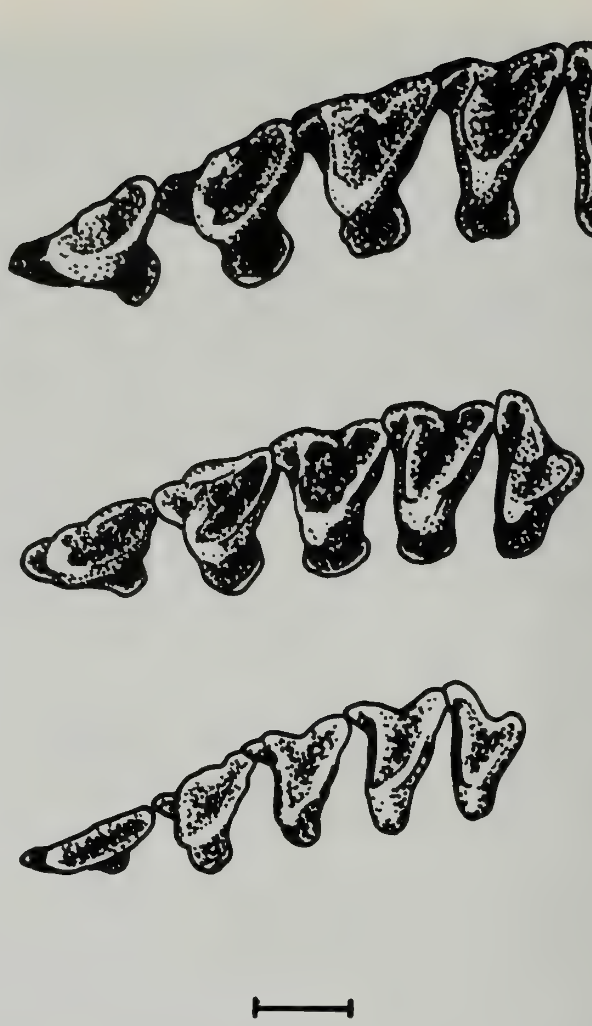

Fig. 7 Occlusal view of left P^3 to M^3 of *Microgale dryas* (top), *M. thomasi* (middle) and *M. gracilis* (bottom). Scale 1 mm.

samples, it is impractical to speculate about possible relationships. Eisenberg & Gould (1970) divided *Microgale* into four behavioural classes on the basis of external morphology. However this classification was challenged by MacPhee (1987) because of redefinition of within–species variation and lack of field study data to support the theory. Specimens of three other species of *Microgale*: *M. cowani*, *M. principula* Thomas, 1926 and *M. talazaci* were collected from the same locality as *M. dryas*. This sympatric association of several different species is apparently common in *Microgale* (see MacPhee, 1987; Nicoll & Rathbun, 1990). Regrettably, some of the species recorded for this locality by Nicoll & Rathbun were based on incorrect preliminary field identifications. Although found in the same habitat, it seems likely that these four species are occupying different ecological niches. Eisenberg & Gould (1970) hypothesised that *M. principula* was a climbing form on the basis of its long tail, which is naked on its distal dorsal surface, and long hindfeet. Although MacPhee (1987), pointed out that there was no evidence of the long tail being prehensile, and studies that might confirm such locomotor behaviour are lacking, these morphological differences do suggest adaptations to a specialised life-style. Studies were made on *M. talazaci* (Eisenberg & Gould, 1970), which show that it is scansorial and shows some burrowing behaviour; its much greater size suggests that it may take larger prey than the smaller species. Since there is no field data for *M. dryas*, no speculation about its ecology or behaviour is attempted here. A species of rice-tenrec, *Oryzorictes talpoides* and two species of rodent, *Eliurus minor* and *E.myoxinus* were also collected from the same locality. The specimens of *M. principula* from this locality represent a northern extension of the recorded range for this species (see MacPhee, 1987).

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Studies on the deep-sea Protobranchia (Bivalvia): the family Nuculidae

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Synopsis. The morphology, geographical distribution and adaptations to life in deep water of ten species of the family Nuculidae (Bivalvia: Protobranchia) from the Atlantic are described. These include four new species. The evolution of the family and the origins of the deep-water species are discussed and the taxonomy of the family reassessed.

INTRODUCTION

This paper forms part of a continuing investigation of the biology of deep-sea protobranch bivalves of the Atlantic (Allen & Hannah, 1989; Allen & Sanders, 1973, 1982; Sanders & Allen, 1973, 1977, 1985). The present study includes an appraisal of the biology, systematics and antiquity of ten species of the deep-sea Nuculidae.

From the time of Linneaus taxonomists have had difficulty in classifying the Nuculidae (eg. Hancock, 1846; Adams, 1856; Sowerby, 1871; Seguenza, 1877; Jeffreys, 1881; Verrill, 1884; Reeve, 1885; Dall, 1886; Hedley, 1902; Iredale, 1931, Schenck, 1934, 1939; Allen, 1954; James, 1972; Lubinsky, 1972). The nuculids were originally regarded as members of the family Arcidae. The type species of the genus *Nucula*, and of the family Nuculidae, is *Arca nucleus* Linné. This is now generally accepted as equivalent to *Nucula nucleus* auct. As with other protobranch groups (Allen, 1978) taxonomic difficulties arise because of the very great conservativeness of shell and body form.

The Subfamily *Nuculacea* has a long fossil record possibly dating from the Ordovician. The apparent stasigenesis involving few cladogenetic events possibly results from an early adaptation to a common homogeneous environment that has persisted throughout much of the zoic period. The magnitude of this early adaptation appears to have left little room for selective pressure change. For example, Levinton & Bambach, (1975) in a comparative study of Silurian and Recent deposit-feeding bivalve communities found that non-siphonate deposit-feeding nuculaceans were dominant forms in the non-compacted, watery sediments of both environments, even though separated by 400 million years. The Silurian counterpart to *Nucula* was a species of *Praenucula* which is similar in size and morphology to *Nucula* and probably had similar life style as an active deposit feeder, just below the sediment-water interface. Rhoads & Young, (1970) found that intensive near-surface reworking of the sediment by non-siphonate protobranchs (*Nucula proxima*) creates an unstable, fluidized sediment. Similar conditions are thought to have been created by *Praenucula* in corresponding Silurian environments (Levinton & Bambach, 1975). According to Rhoads & Young, (1970) this has the effect of excluding siphonate forms and suspension feeders from the deposit-feeder biotope. The reduced competition resulting from the exclusion by non-siphonate protobranchs of more advanced forms, especially those of the massive post-Palaeozoic radiation of infaunal, siphonate heterodonts (Stanley, 1968), may further help to explain why the nuculoid forms have persisted virtually unchanged for such an enormous period of time. This ability to thrive in fluid sediments also pre-adapted the nuculids for a deep-sea existence.

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The nuculids have been regarded as being close to the stem stock of many proposed phylogenies of the bivalves (eg. Pelseneer, 1911; Yonge, 1939) and, even though they are not now regarded as being similar to the ancestral bivalve (Atkins, 1938; McAlester, 1964; Allen & Sanders, 1969; Morris & Fortey, 1976; Babin, 1977; Allen, 1985), they are probably close to the ancestral stock of the subclass Protobranchia. An examination of the fossil record has been carried out to endeavour to establish which of the extant species are close to the ancestral stock furthermore, because the nuculids are such an archaic group it was thought that it might provide a contribution to the debate on the origin and antiquity of deep-sea fauna.

MATERIAL & METHODS

Specimens used in this study were sampled as follows: 1) Marine Biological Association of the United Kingdom (1967)—Bay of Biscay, R.V. 'Sarsia'; 2) Institute of oceanographic Science, U.K. (1968)—between Fuerteventura and the West African coast, RRs 'Discovery'; 3) Centre National de tri d'Oceanographic Biologique, France—Walda (1971), between Nigeria and the Angola, R.V. 'Jean Charcot'; Biogas (1972–74)—Bay of Biscay, R.V. 'Jean Charcot', R.V. 'La Perle' and R.V. 'Cryos'; Incal (1976), Rockall Trough and the North East Atlantic, R.V. 'Jean Charcot'; 4) Woods Hole Oceanographic Institute, U.S.A.—North America Basin (1961–73), Gayhead-Bermuda transect, R.V. 'Atlantis', R.V. 'Atlantis II', R.V. 'Chain', and R.V. 'Knorr'; Cape Verde Basin (1967), between Dakar and Recife, R.V. 'Atlantis II'; Angola Basin (1968), between Walvis Bay and Luanda, R.V. 'Atlantis II'; Argentine Basin (1971), transect shelf slope break to abyss, R.V. 'Atlantis II'; Guiana Basin (1972), transect shelf slope break to abyss, R.V. 'Knorr'; West European Basin (1972), between Ireland and Woods Hole, R.V. 'Chain'; 5) Scottish Marine Biological Association (1973–86), Rockall Trough, R.R.S. 'Challenger'; 6) Naval Ocean Research and Development Activities N.S.T.L. Station, U.S.A. (1981), Venezuela Basin, USNS 'Barlett'.

The vast majority of samples were obtained using various forms of epibenthic sledge (ES/ET/ED). The remaining samples were obtained using a Sanders Dredge (SD), Agassiz Trawl (AT), Anchor Dredge (AD), Otter Trawl (OT), Anchor Box Dredge (ABD), Spade Box Corer (SBC) and Beam Trawl (CP = chalût à perche). The samples were elutriated on board using sieves (mesh 0.42 mm USA and U.K., 0.25 & 0.50 mm France), fixed in 4% or 10% formal saline (4% formaldehyde in the case of S.M.B.A. samples) and then after 24 hours, washed and transferred to 70% or 95% ethanol.

Histological Procedures

For taxonomic comparison, distortion of the sections had to be reduced to a minimum. Much distortion occurs with excessive heat during wax infiltration and section flattening. This was minimized by using low melting point polyester wax (37°C) (Steedman, 1957). This wax is miscible in alcohol and obviates the need to use xylene prior to hydration thus further reducing distortion. Most sections were cut at 25 microns, below this they fail to expand to their original proportions during flattening process (Aumonier, 1938). Standard, Mayer's haematoxylin was used with eosin as a counter stain and supplemented by sections stained with Azan to differentiate between acidophilic and basophilic cytoplasm (Humason, 1967). for muscle and connective tissue, the trichrome staining methods of Pantin, (1946) and Pollak, (1944) were used.

Three-dimensional reconstruction requires a sequence of perfectly alignable serial sections. At least two static reference points are necessary and which run the length of the embedded specimen. The technique of Pusey, (1939) was found to be the most satisfactory. The block was painted with an indelible colloidal stain made up of Indian ink and bile salts. The procedure has been used mainly to determine configuration of the coils of the hindgut.

Stained whole mounts were also prepared using Ehrlich's haematoxylin.

Shape Analysis: Specimens from nine abyssal Atlantic Basins were drawn in lateral view using a Wild M5 microscope with a drawing attachment. In the case of large samples specimens were selected randomly by spreading them over graph paper and then selecting them by X, Y co-ordinates specified by computer-generated random numbers. Using a Hewlett Packard Shape Analysis System the drawings were analysed with reference to the area and perimeter of each shape. Then, a series of linear measurements were made (Fig. 1), quantifying nine variables in each specimen. A further 'dummy' variable was added recording the presence or not of external radial shell markings. Analysis was by computer-based statistics. Standardization of the data to z-scores was achieved by substracting the mean (X) from each variate (Y) and dividing by the standard deviation (S) to give the rth standardized value

$$Zr = (Yr - X)/S$$

The data set so derived has a mean of zero and a standard deviation of one. In morphometric terms this transformation has three advantages. First, all values less than the mean have a negative sign and all greater are positive, with the result that distance (or degree of similarity) between individuals can be inspected visually. Second, it is possible to relate the distance from one individual to another or from one individual to a point of reference, (eg. a centroid) independent of the unit of measurement of the original data. Third, for multivariate analysis it is an advantage to have a standard variance of one in that each variable is on the 'equal footing' in a geometrical sense such that each variable is treated symmetrically and independent of the variance. It also was found that because the range in size of the specimens was

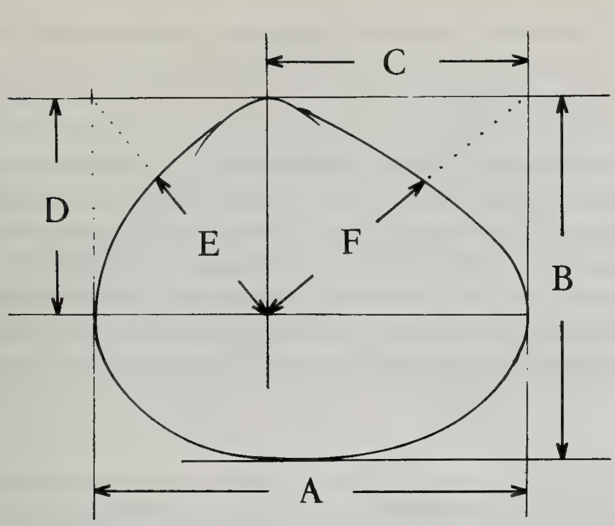

Fig. 1 Measurements (mm) A, B, C, D, E, F & G together with the area perimeter length for each specimen.

large it was necessary to eliminate a size effect by dividing each linear variable by length, and area by length squared. This is important because if shape differences are subtle (as many are) then size will tend to predominate in any clustering procedure and clusters will form on the basis of size rather than shape.

The morphometric data was subjected to multivariate analysis using the ordination technique of principal co-ordinate analysis (Gower, 1966). This was carried out using the software package GENSTAT on the Edinburgh University mainframe computer. Like principal component analysis, principal co-ordinates analysis is used to reduce dimensionality but, instead of being based on a P × P dispersion or correlation matrix where there are measurements on P variates for each of N individuals, it is based on an N × N association matrix and is therefore a Q rather than an R technique (Sokal & Sneath, 1963). The procedure generates a set of vectors that are a linear combination of the individuals scores. These are the principal co-ordinates. If the first K principal co-ordinates give an adequate representation of the data in K dimensions, the remaining N–K can reasonably be disregarded as uninformative.

Abbreviations to text figures

aa	anterior adductor muscle
apr	anterior pedal retractor muscle
by	'byssal' gland
cg	cerebral ganglion
dd	digestive duct
dh	dorsal hood
di	digestive diverticula
ft	foot
ga	gill axis
gi	gill
gs	gastric shield
ht	heart
hy	hypobranchial gland
ky	kidney
ma	mantle
oe	oesophagus
ov	ovary
pa	posterior adductor muscle
pb	palp proboscis
pg	pedal ganglion
pp	palp
ppr	posterior pedal retractor muscle
ps	posterior sorting area
sr	sorting ridges
ss	style sac
st	stomach
ts	testis
ty	typhlosole
vg	visceral ganglion

TAXONOMY

Early systematic studies on the Nuculidae (eg. Montagu, 1808; Reeve, 19885; Adams, 1856) were based on differences in shell morphology. A more-detailed attempt was made by Schenck, (1939) who also classified Recent and fossil species by shell characters alone, though he pointed out that it was impossible to say what characters should be accorded the greater weight, and whether emphasis should be placed on 'soft or hard part' morphology. Moore, (1931a, 1931b) distinguished between shallow-water nuculid species on the basis of the pattern of grooves on the faecal pellets, however Allen, (1954) was to show that this was not an infallible method. Indeed, sections of the hindgut show that the pellets of deep-sea species have no systematic value usually being round or oval in cross-section and without distinctive grooves. Heath, (1937) described variations in the musculature and the digestive system of various species and found that the configuration of the hindgut could be used as a consistent diagnostic feature. This remains true (Allen, 1978), however the hindgut of deep-sea nuculid species is usually smaller in diameter and far more extensively coiled as compared with shallow-water species, and to determine differences, delicate dissection is required, supported by examination of small whole-mount specimens and sections. Furthermore, there appears to be a degree of intraspecific variation. The musculature of deep-sea species *per se* has little systematic value but differences in the orientation of the body and the size and shape of the foot are reflected in the deposition of the pedal musculature. Interspecific differences in the morphology of the stomach were also noted.

Morphological orientation in bivalves is frequently related to a series of axes, (Allen, 1985). Definitions are by no means consistent, thus, Fischer, (1886) defined the antero-posterior axis as a straight line touching the lower margins of the adductor muscles, whereas, Jackson, (1890) considered it to pass through the mouth and the middle of the posterior adductor muscle. The cardinal or hinge axis as distinct from the body axis is most used as the basic criterion for orientation, the latter being assessed by the change from parallel of the hinge and oro-anal axes (Kauffmann, 1969). Unfortunately, the hinge axis is not easily determined in the Nuculidae. Differing orientations of the foot appear to be correlated with the degree of alignment of the adductor muscle axis as compared with the axis through cerebral and pedal ganglia (Fischer, 1886). Such axes cannot be determined with mathematical precision and cannot be used in a strict taxonomic sense, nevertheless they show how interspecific transformations are related to various anatomical reference points.

The family is very conservative with regard to its body anatomy. Thus, Schenck, (1944) working with *Nucula tamatavica* and Heath, (1937) with *N. nucleus* found that these species could not be separated from others on the basis of their anatomy. Similarly Moore, (1931a) and Allen, (1954) could not find any significant anatomical differences between the British species of *Nucula*. Shell morphology, therefore, remains of paramount importance to the taxonomy of the Nuculidae.

On the basis of shell morphology, Schenck, (1934) split the nuculids into three main 'Taxonomic Units'.

(A) Forms with crenulate inner ventral margins.
(1) *Nucula* Lamarck, (1799)
(2) *Pronucula* Hedley, (1902)
(3) *Pectinucula* Quenstedt, (1930)
(4) *Linucula* Marwick, (1931)
(5) *Deminucula* Iredale, (1931)
(6) *Lamellinucula* Schenck, (1944)
(7) *Gibbonucula* Eames, (1951)

(B) Forms with smooth inner ventral margins.
(1) *Ptychostolis* Tullberg, (1991)
(2) *Nuculoma* Cossmann, (1907)
(3) *Nuculopsis* Girty, (1911)
(4) *Nuculoidea* Williams & Breger, (1916)
(5) *Nuculopsis* Woodring, (1925)
(6) *Leionucula* Quenstedt, (1930)
(7) *Palaeonucula* Quenstedt, (1930)
(8) *Ennucula* Iredale, (1931)
(9) *Brevinucula* Thiele, (1934)
(10) *Austronucula* Powell, (1939)
(11) *Trigonucula* Ichikawa, (1949)
(12) *Habonucula* Singh & Kanjilal, (1977)
(13) *Condylonucula* Moore, (1977)

(c) Forms with divaricate sculpture.
(1) *Acila* H. & A. Adams, (1958)
(2) *Truncacila* Schenck, (1931)

Thereafter, Cox, (1940) described species such as *Nucula obliqua* Lamarck, *Nucula expansa* Reeve and *Nucula superba* Hedley, as intermediate between 'crenulate' and 'non-crenulate' forms in that they possessed very fine crenulations only visible with microscopic aid. Vokes, (1949) who found a similar condition in the Palaeozoic species *Nuculoidea opima* Hall suggested that such species should be placed in a separate group.

Many of the taxa listed above, are known only as fossils. Of these Thiele, (1934) was of the opinion that *Ennucula* and *Leionucula* are congeneric and Allen & Hannah, (1986) synonymized *Linucula* with *Nucula*, ajudged that *Pronucula* is a subgenus of *Nucula* and that *Nuculopsis* Woodring (*non* Girty), *Leionucula, Ennucula* and *Austronucula* are synonymous with *Nuculoma*.

On the basis of shell structure, Recent non-divaricate species have been divided into two genera, *Nucula* and *Nuculoma* (Poel, 1955). species in which the outer shell layer is constructed of radial elements and, consequently, have a crenulate inner ventral shell margin are included in the genus *Nucula*. Those with a uniform, non-radial, structure with a smooth inner ventral shell margin are included in *Nuculoma*. Taylor *et al*., (1969) describe the shell of *Nucula* as being composed of three layers of aragonite, the inner being nacrous. Unfortunately, Taylor *et al*., (1969) did not report on *Nuculoma*, however, we can confirm that *Nuculoma* species described here have an inner nacrous layer. It has been assumed that species of the Nuculacea and Nuculanacea can be distinguished on the basis that nuculaceans have an inner nacreous layer, which is absent in nuculanceans, however, Moore (1977) in his description of a tropical, shallow-water nuculacean *Condylonucula* states it is without an inner nacreous layer. Similarly Cox, (1959) states that early fossil members of the Nuculacea and Nuculanacea are not easily distinguished in that some Jurassic species of *Nuculana* have an inner nacreous layer. All deep-sea nuculaceans so far examined have an inner nacreous layer.

CLASSIFICATION

As a result of this study on the shell morphology and anatomy of the Nuculidae of the deep Atlantic and on the Recent and fossil material from the Natural History Museum, London (BM(NH)) and elsewhere, and examination of descriptions in the literature, a new listing of the *extant* genera of the family Nuculidae has been arrived at.

Family **NUCULIDAE** Gray, 1824

Genus **NUCULOIDEA** Williams & Breger, 1916

TYPE SPECIES: **Cucullea opima** Hall, (1843)
Shell ovate, inequilateral with concentric sculpture; faintly prosogyral; inner ventral margin not crenulate but with internal marginal micropectinations; resilifer perpendicular to hinge plate; inner nacreous layer present.

Originally Williams & Breger, (1916) proposed the subgeneric name *Nuculoidea* for Palaeozoic species of *Nucula* having a non-crenulate inner ventral margin and with other characters intermediate between those of the extinct family Ctenodontidae and the Recent members of the family Nuculidae. These latter include a cartilage pit as found in *Ctenodonta albertina* Ulrich (upper Ordovician). Williams & Breger, (1916) divided the species of *Nuculoidea* into three groups each based on a described species: (1) *Nuculoidea opima* (Hall) with umbones twisted to a vertical position or faintly prosogyrate, shell usually anteriorly elongate and semi-lunate; (2) *Nuculoidea aquisgranensis* (Beuschausen) with opisthogyrate umbones, anterior and convexly rounded and usually the larger, posterior outline semi-lunuliferous; (3) *Nuculoidea niotica* (Hall) with opisthgyrate umbones, posterior margin truncate and nearly vertical, anterior margin also nearly straight, producing a characteristic vertically triangular outline. Later, McAlester, (1962) upgraded *Nuculoidea* to generic rank. Similarly, Soot-Ryen, (1964) and Liljedahl, (1983, 1984) in a systematic account of nuculoid pelecypods from the Silurian (Palaeozoic) formations of gotland described a number of nuculoids with characters common with the *Nuculoidea opima* group and raised these species to the generic rank.

We are reluctant to create a new genus for Recent forms that match the description given above, particularly in regard to the faintly prosogyral nature of the beaks, the micropectinate margin and the vertical ligament. Furthermore, this relates to the fact that many deep-sea bivalves belong to groups with a long geological record.

Genus **NUCULOMA** Cossmann, 1907

TYPE SPECIES: **Nucula castor** d'Orbigny, (1850)
Shell ovate or triangular, smooth or with concentric sculpture; opisthogyral; ventral margin not crenulate as seen externally but may be microscopically crenulate internally corresponding with marginal limits of radial shell elements; resilifer oblique to hinge plate; inner nacrous layer present.

Cossmann, in Cossmann & Thiery, (1907) proposed the subgeneric name *Nuculoma* for Jurassic nuculids characterized for the most part by a narrow oblique chondrophore. Later Schenck, (1934) raised *Nuculoma* to generic rank.

Genus **BREVINUCULA** Thiele, 1934

TYPE SPECIES: **Nucula guineensis** Thiele, (1931)
Shell deeply triangular with smooth surface; opisthogyral; inner ventral margin not crenulate; resilifer absent or very small, inner nacrous layer present.

Thiele, (1934) originally proposed the subgeneric name *Brevinucula* for a deep-sea species *Nucula guineensis* (p. 83) from the Gulf of Guinea which was later synonymized with *Nucula verrilli* (Verrill & Bush, 1898).

Genus **CONDYLONUCULA** Moore, 1977

TYPE SPECIES: **?Condylonucula cynthiae** Moore, (1977)
Shell very robust, ovate with concentric sculpture, heavily sculptured cap-like prodissoconch; opisthogyral; inner ventral margin not crenulate; resilifer perpendicular to hinge plate; inner nacreous layer absent.

Species of *Condylonucula* are confined to shallow-water sediments of the tropical western Atlantic.

Genus **NUCULA** Lamarck, 1799

TYPE SPECIES: **Arca nucleus** Linné, (1758)
Shell ovate-triangular, inequilateral with reticulate sculpture; opisthogyral; inner ventral margin crenulate; hinge line angulate; resilifer oblique to hinge plate; inner nacrous layer present.

Genus **DEMINUCULA** Iredale, 1931

TYPE SPECIES: **Nucula praetenta** Iredale, (1931)
Shell triangular with reticulate sculpture; opisthogyral; inner ventral margin crenulate; hinge line angulate; resilifer not well-defined, inner nacrous layer present.

Schenck, (1934) questioned whether *Deminucula* should be included in the *Nuculidae* in that the original specimens (Smith, 1891) showed that they were without a 'chondrophore'. A possible explanation of the difference between *Deminucula* and *Nucula* is that there has been retention of juvenile shell characteristics into adulthood (neoteny) in *Deminucula* (p. 67). This is evident when *D. atacellana* is compared with the juveniles of a shallow water species such as *Nucula sulcata*.

Genus **PRONUCULA** Hedley, 1902

TYPE SPECIES: **Pronucula decorosa** Hedley (1902)
Shell triangular with reticulate sculpture; opisthogyral; inner ventral margin crenulate; hinge line arched; resilifer perpendicular to hinge plate, inner nacrous layer present.

This genus differs from *Nucula* in having an arched instead of an angulate hinge line, the hinge teeth series do not overlap beneath the umbos, and the resilifer is perpendicular rather than oblique to the hinge plate. Since the description by Hedley, (1902), Cotton, (1930) and Marwick, (1931) and Clarke, (1961) have described several other Recent and Tertiary species from the southern hemisphere.

Genus **ACILA** (Adams & Adams, 1858)

TYPE SPECIES: **Nucula divaricata** Hinds, (1843) Shell ovate-triangular with divaricate sculpture; opisthogyral; hinge line arched; inner ventral margin crenulate; resilifer oblique to hinge plate; inner nacrous layer present.

Adams & Adams, (1858) proposed the generic name *Acila* for nuculid species mainly characterized by a divaricate sculpture. Extant species are restricted to the Indo-Pacific and to relatively shallow depths (Schenck, 1934).

ATLANTIC DEEP-SEA SPECIES OF THE FAMILY NUCULIDAE

Deminucula atacellana (Schenck, 1939)

Figs 2–4, 5a, 6, 7a

TYPE LOCALITY: Porcupine St 16, off NW Coast of Ireland, 1476 and 1215 fms. Designated Schenk (1939).

TYPE SPECIMEN: Holotype: not designated, Lectotype: USNM No. 197154 selected by Schenck, (1939) Pl. 5, figs. 4, 5, 9, 10, 13, 16. (7 specimens from Atlantis II, Sta. 131, 39°38.5′N. 70°36.5′W, 2178 m lodged in BM(NH) No. 1990010). *Nucula reticulata* Jeffreys, 1876, p. 429; 1879, p. 583; (*non* Hinds, 1843); Smith, 1885, p. 229.

Nucula cancellata Jeffreys, 1881, p. 951; (*non* Meek & Hayden, 1856, p. 85); Verrill, 1884, p. 280, 285; Dall, 1890, p. 258; Dautzenberg & Fischer, 1897, p. 203, 204; Verrill & Bush, 1897, p. 854, pl. 81, Fig. 3, pl. 86, Fig. 5; Johnson, 1934, p. 15; Dautzenberg, 1927, p. 288.

Nucula (Nucula) atacellana Schenck, 1939, p. 27, pl. 5, Figs 4, 5, 8, 10, 13, 16.

DEPTH RANGE: 1102–4938 metres.

MATERIAL

Cruise	Sta	Depth (m)	No	Lat	Long	Gear	Date
			NORTH AMERICA BASIN				
Atlantis II	62	2496	82	39°16.0′N	70°33.0′W	ET	21.08.64
	64	2886	1	38°46.0′N	70°06.0′W	ET	21.08.64
	73	1470	361	39°46.5′N	70°43.3′W	ET	25.08.64
Chain	76	2862	1	39°38.3′N	67°57.8′W	ET	29.06.65
	77	3806	54	38°00.7′N	60°16.0′W	ET	30.06.65
	78	3828	12	38°00.8′N	69°18.7′W	ET	30.06.65
	85	3834	69	37°59.2′N	60°26.2′W	ET	5.07.65
	87	1102	48	39°48.7′N	70°40.8′W	ET	06.07.65
	87	1102	48	39°48.7′N	70°40.8′W	ET	06.07.65

Cruise	Sta	Depth (m)	No	Lat	Long	Gear	Date
Atlantis II	115	2051	2131	39°39.2′N	70°24.5′W	ET	16.08.66
Atlantis II	126	3806	3	39°37.0′N	66°47.0′W	ET	24.08.66
	128	1254	12	39°46.5′N	70°45.2′W	ES	16.12.66
	131	2178	1022	39°38.5′N	70°36.5′W	ES	18.12.66
Chain	210	2064	409	39°43.2′N	70°49.5′W	ES	22.02.69
	335	3882	3	40°23.3′N	46°30.0′W	ES	31.08.72
Knorr	340	3264	25	38°14.4′N	70°20.3′W	ES	24.11.73
WEST EUROPEAN BASIN							
Chain	313	1500	15	51°32.2′N	12°35.9′W	ES	17.08.72
	316	2209	531	50°57.7′N	13°01.3′W	ES	18.08.72
	318	2506	7	50°27.3′N	13°20.9′W	ES	19.08.72
	321	2890	4	50°12.3′N	13°35.8′W	ES	20.08.72
Incal	CP08	2644	1	50°14.7′N	13°13.5′W	CP	27.07.76
ROCKALL TROUGH							
Challenger	2	2857	2	55°04.0′N	12°33.0′W	ES	04.06.73
	3	1997	1	56°46.0′N	10°02.0′W	ABD	05.06.73
	4	1993	24	56°52.0′N	10°01.0′W	ES	05.06.73
	6	2900	547	55°02.0′N	12°29.0′W	ES	02.07.73
	8	2900	5	54°45.0′N	12°10.0′W	ES	03.07.73
	10	2540	147	56°37.0′N	11°04.0′W	ES	04.07.73
	12	2076	6	56°49.0′N	10°15.0′W	ES	20.09.73
	13	1842	8	56°45.0′N	09°50.0′W	ABD	22.09.73
	15	1632	13	56°44.0′N	09°28.0′W	ES	22.09.73
	18	1392	16	56°44.0′N	09°20.0′W	ES	22.09.73
	27	2880	456	54°40.0′N	12°16.0′N	ES	03.11.73
	34	2515	536	56°36.0′N	11°30.0′N	ES	10.05.75
	48	2875	1	55°04.0′N	12°04.0′W	SBC	07.09.75
	49	2875	1	55°03.0′N	12°05.0′W	SBC	07.09.75
	51	2875	1	55°03.0′N	12°03.0′W	SBC	07.09.75
	55	2878	52	54°40.0′N	12°16.0′W	ES	17.11.75
	56	2886	105	54°40.0′N	12°16.0′W	ES	01.03.76
	57	2950	67	54°41.0′N	12°23.0′W	ES	21.06.76
	58	2900	2	54°41.0′N	12°17.0′W	SBC	21.06.76
	59	2900	96	54°40.0′N	12°20.0′W	ES	21.06.76
	63	1800	1	56°37.0′N	09°49.0′W	SBC	25.06.76
	69	1050	24	59°39.0′N	07°12.0′W	ES	02.07.76
	110	2886	92	54°41.0′N	12°14.0′W	ES	22.10.76
	111	2886	104	54°40.0′N	12°16.0′W	ES	22.10.76
	118	2910	68	54°39.0′N	12°14.0′W	ES	28.01.77
	121	2910	1	54°37.0′N	12°09.0′W	AT	29.01.77
	124	2900	184	53°30.0′N	13°15.0′W	AT	30.01.77
	135	2900	158	54°39.0′N	12°16.0′W	ES	07.08.77
	137	2900	69	54°34.0′N	12°19.0′W	ES	22.02.78
	174	2885	1	54°44.0′N	12°18.0′W	SBC	22.05.80
	176	2245	168	57°15.0′N	10°26.0′W	ES	28.05.80
	185	2907	32	54°44.0′N	12°15.0′W	ES	10.04.81
	231	2898	69	54°42.0′N	12°12.0′W	ES	17.05.83
Incal	DS01	2091	3	57°59.7′N	10°39.8′W	SD	15.07.76
	DS02	2081	1	57°58.8′N	10°48.5′W	SD	16.07.76
	CP03	2466	4	55°38.0′N	11°64.4′W	CP	17.07.76
	CP04	2483	5	56°33.2′N	11°11.3′W	CP	17.07.76
	DS06	2491	24	56°26.6′N	11°10.5′W	DS	18.07.76
	DS07	2884	37	55°00.0′N	12°31.0′W	SD	19.07.76
	CP05	2884	4	55°00.0′N	12°29.0′W	CP	19.07.76
	CP06	2888	4	55°02.3′N	12°40.3′W	CP	19.07.76
	CP07	2895	4	55°03.4′N	12°49.2′W	CP	20.07.76
	DS09	2897	62	55°07.7′N	12°52.6′W	SD	20.07.76
	CP08	2644	1	50°14.7′N	13°13.5′W	CP	27.07.76
BAY OF BISCAY							
Sarsia	S44	1739	14	43°40.8′N	03°35.2′W	ES	16.07.67
	S50	2379	1	43°46.7′N	03°47.8′W	ES	18.07.67
	S65	1922	3	46°15.0′N	04°50.0′N	ES	25.07.67
Biogas II	DS32	2138	2	47°32.2′N	08°05.3′W	SD	18.04.73
Biogas III	DS37	2110	1	47°31.8′N	08°34.6′W	SD	24.08.73
	DS41	3548	1	47°28.3′N	09°07.2′W	SD	26.08.73
	DS49	1845	29	44°05.9′N	04°15.6′W	SD	01.09.73
	DS50	2124	1	44°08.9′N	04°15.9′W	SD	01.09.73
Biogas IV	DS51	2430	5	44°11.3′N	04°15.4′W	SD	18.02.74
	DS52	2006	30	44°06.3′N	04°22.4′W	SD	18.02.74
	DS62	2175	1	47°32.8′N	08°40.0′W	SD	26.02.74
	DS63	2126	1	47°32.8′N	08°35.0′W	SD	26.02.74
	DS64	2156	3	47°29.2′N	08°30.7′W	SD	26.02.74
Biogas V	CP07	2170	7	44°09.8′N	04°16.4′W	CP	21.06.74
Biogas VI	DS71	2194	3	47°34.3′N	08°33.8′W	SD	20.02.74
	DS86	1950	105	44°04.8′N	04°18.7′W	SD	31.10.74
	DS87	1913	79	44°05.2′N	04°19.4′W	SD	01.11.74
	DS88	1894	7	44°05.2′N	04°15.7′W	SD	01.11.74
Polygas	DS18	2138	1	47°32.2′N	08°44.9′W	SD	22.10.72
	DS25	2096	5	44°08.2′N	04°15.7′W	SD	01.11.72
	DS26	2076	12	44°08.2′N	04°15.0′W	SD	01.11.72
GUYANA BASIN							
Knorr	293	1518	9	08°58.0′N	54°04.3′W	ES	27.02.72
	299	2076	2	07°55.1′N	55°42.0′W	ES	29.02.72
	301	2500	12	08°12.4′N	55°50.2′W	ES	29.02.72
	303	2953	7	08°28.8′N	56°04.5′W	ES	01.03.72
CANARIES BASIN							
Discovery	6697	1564	3	27°57.0′N	13°46.0′W	ED	15.03.68
	6701	1934	6	27°45.2′N	14°13.0′W	ED	16.03.68
	6704	2129	14	27°44.9′N	14°25.0′W	ED	17.03.68
CAPE VERDE BASIN							
Atlantis II	141	2131	3	10°30.0′N	17°51.5′W	ES	05.12.67
	142	1796	48	10°30.0′N	17°51.5′W	ES	05.12.67
	148	3828	1	10°37.0′N	18°14.0′W	ES	07.12.67
	149	3861	2	10°30.0′N	18°18.0′W	ES	07.02.67
GUINEA BASIN							
Walda	DS20	2514	1	02°32.0′S	08°18.1′E	SD	–
	DS29	3547	2	02°57.0′S	04°28.1′E	SD	–
ANGOLA BASIN							
Atlantis II	195	3797	20	14°50.0′S	09°54.0′E	ES	19.05.68
	196	4630	6	10°29.0′S	09°04.0′E	ES	21.05.68
	197	4595	34	10°04.0′S	09°04.0′E	ES	21.05.68
	198	4566	16	09°47.0′S	10°29.0′E	ES	21.05.68
	200	2754	1	09°43.5′S	10°57.0′E	ES	22.06.68
	201	2031	8	09°05.0′S	12°17.0′E	ES	23.05.68
ARGENTINE BASIN							
Atlantis II	243	3822	213	37°36.8′S	52°23.6′W	ES	14.03.71
	245	2707	77	36°55.7′S	53°01.4′W	ES	14.03.71
	256	3917	356	37°40.8′S	52°19.3′W	ES	24.03.71
	259	3305	862	37°13.3′S	52°45.0′W	ES	26.03.71

SHELL DESCRIPTION

The original description by Jeffreys, (1876) is detailed and accurate and only a summary description is given here.

Shell ovate, ventricose, lustrous, translucent, equivalve, inequilateral; umbo posterior to midline, slightly opisthogyrate or orthogyrate; when postero-dorsal margin is orientated vertically the antero-dorsal margin is above horizontal; lunule and escutcheon not obvious, hinge teeth often visible through thin dorsal area; surface with fine concentric ridges which disappear towards the umbo, radial striations give impression of reticulation; chondrophore absent, resilifer inconspicuous, not oblique; hinge plate moderately broad; teeth chevron-shaped, the number varies with the size of the specimen (Fig. 2). Thus a shell 3.86 mm in length has 8 teeth in the anterior series and 5 in the posterior and for shells of 2.64 mm and 1.46 mm in length the numbers of teeth are 6/4 and 4/2 respectively.

There appears to be a continuous gradation in the external characters of *Deminucula atacellana* and of *Nucula callicre-*

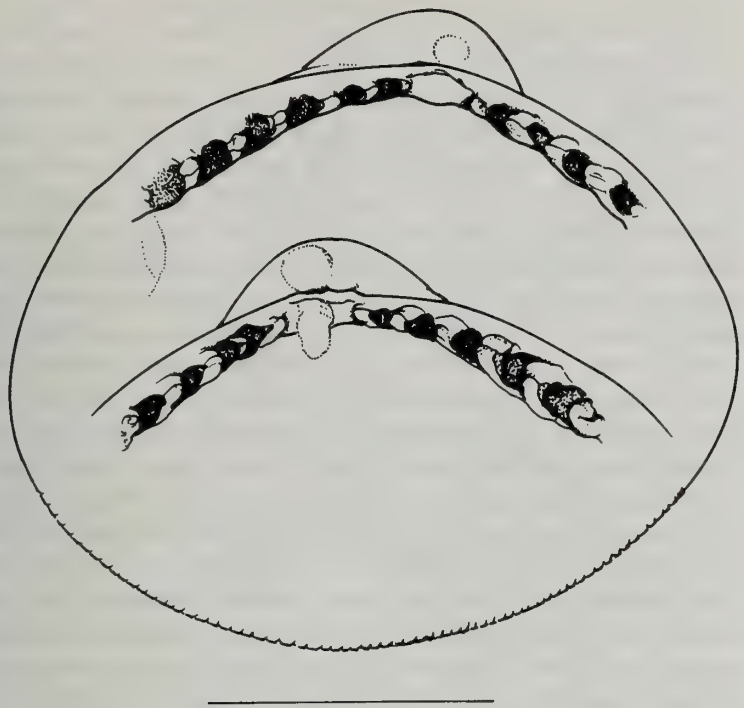

Fig. 2 *Deminucula atacellana*. Internal view of the left valve and hinge region of the right valve of a shell from Station 131. (Scale = 1.0 mm).

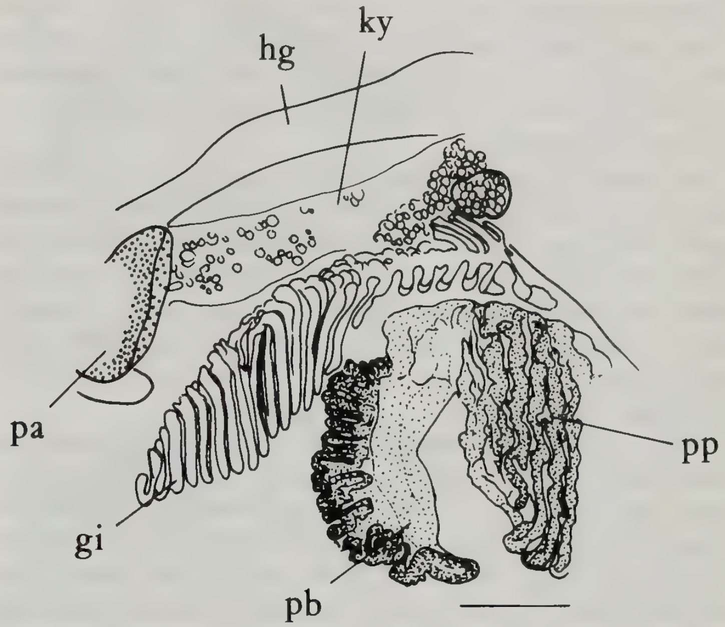

Fig. 4 *Deminucula atacellana*. Enlarged lateral view as seen from the right side of the gill and surrounding organs. (Scale = 0.2 mm; for key to abbreviations see p.63).

demna (Fig. 7b) (p. 69). While Dall, (1890) regarded *N. callicredemna* as belonging to the group which includes *D. atacellana*, both Schenck, (1939) and Knudsen, (1970) believed the species to be conspecific with *D. atacellana*. In contrast James, (1972) states that there is a change in the shape of the outline of *N. callicredemna* with age with the shell becoming more ovate. This allomorphic variation taken with the fact that adult populations of *D. atacellana* also show a large amount of variation in shape is probably the reason why authors have debated the species. In fact, some mature specimens of *D. atacellana* appear identical to small specimens of *D. callicredemna* however, small immature specimens of *N. callicredemna* do not look like large mature specimens of *N. callicredemna* nor of *D. atacellana* of similar length. The small immature *N. callicredema* are far more triangular in shape (James, 1972) (Fig. 7). Mature specimens of *N. callicredemna* and *D. atacellana* can be clearly separated on the basis of the internal shell morphology, and apart from the features outlined in the shell descriptions of the two species, they also differ in that mature specimens of *D. atacellana* are typically deminuculoid and without a well-defined resilifer (Fig. 4), whereas mature specimens of *N. callicredemna* have a well-developed chondrophore (Fig. 8). *N. callicredemna* grows to a much larger size than does *D. atacellana*.

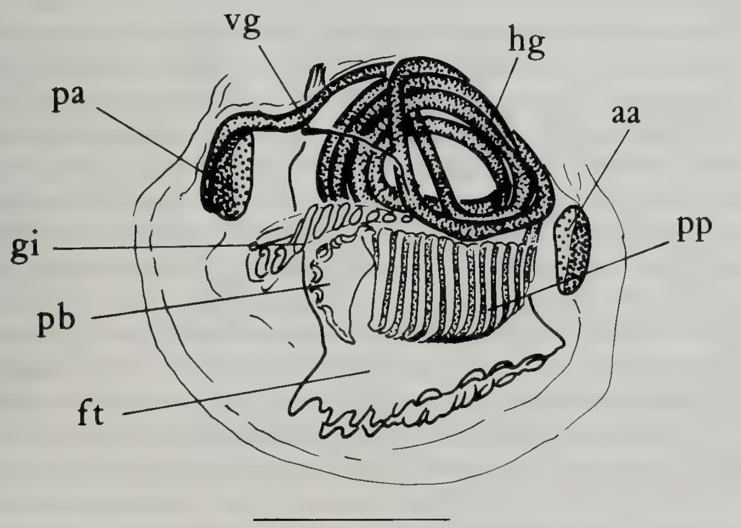

Fig. 3 *Deminucula atacellana*. The gross anatomy as seen from the right side of a whole mount with the shell removed. (Scale - 1.0 mm; for key to abbreviations see p.63).

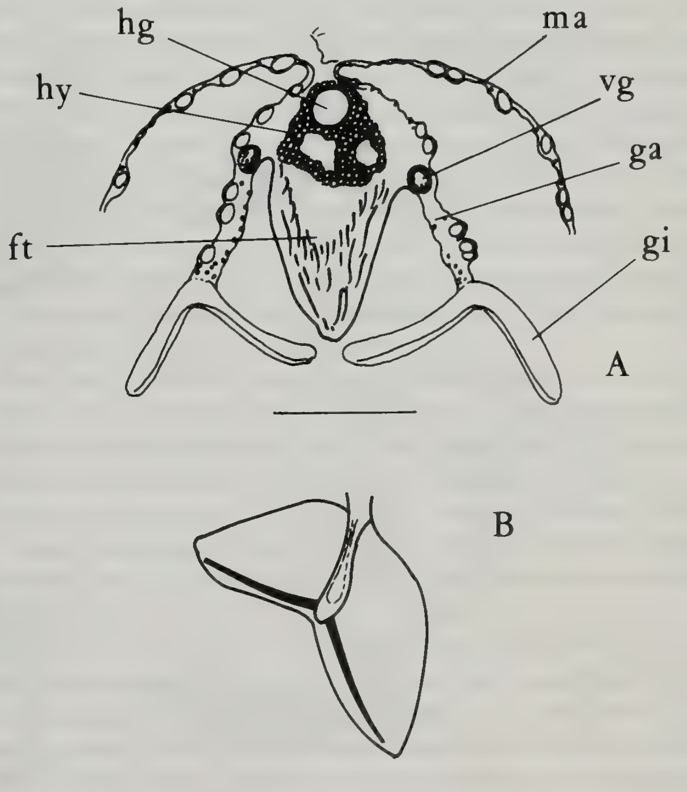

Fig. 5 A. *Deminucula atacellana*. Semidiagrammatic view of a transverse section immediately anterior to the posterior adductor; B. *Nucula delphinodonta* inner and outer gill plates as drawn by Drew 1901. (Scale = 0.5 mm; for key abbreviations see p.63).

INTERNAL MORPHOLOGY

D. atacellana being the most common abyssal nuculid, is used to provide a basic account of morphology against which the other species can be described and compared. Particular emphasis is placed on features that show adaptation to its deep-water existence.

The mantle edge of *D. atacellana* is relatively unmodified and typically consists of an inner muscular lobe, a middle sensory lobe and an outer lobe which secretes the outer layer of the shell. The periostracum arises from the junction of the outer and middle layer and there is a broad zone of attachment of the pallial muscle. Trichrome staining shows numbers of gland cells scattered throughout the outer and inner epithelium of the mantle.

Each labial palp is made up of a proboscis, pouch and paired lamellae (Figs 3a & 4). They are not greatly larger in overall size to those of more shallow-water nuculid species (Allen, 1978) and their structure compares well with the description given by Hiraska, (1927) for *Nucula nucleus*. The inner surfaces are covered with a layer of columnar epithelial cells with long cilia and with a cytoplasm which is strongly acidophilic. The epithelial cells of the outer surfaces are squamous. The outer surfaces are smooth whilst the inner surfaces are ridged dorso-ventrally. The fine structure of the ridges compares well with that of *N. nucleus*. The ridges get smaller towards the anterior part of the palp and their structure in cross-section changes slightly. The number of ridges varies and ranges from 12 in specimens ca. 1 mm total length to 27 in specimens ca. 3 mm total length.

The palp proboscis extending from the posterior dorsal limit of the palps is muscular and contractile. The form in life is difficult to determine for in preserved specimens they are always in an extreme state of contraction (Fig. 4). Nevertheless, they have a similar morphology to that of *Nucula delphinodonta* (Drew, 1901), and *Nucula nucleus* (Hirasaka, 1927). Morphologically they are an extension of the distal oral groove and a shallow V-shape in section. The concave surface and its margins consist of a single layer of columnar epithelial cells with long cilia. The convex surface has a single layer of more cuboidal epithelial cells whch appear to be devoid of cilia. Trichrome staining shows large numbers of mucous secreting cells, especially in the concave surface. Each proboscis has well-developed longitudinal muscle fibres amongst connective tissue. The fibres are continuous with the musculature of the body wall and are asymmetrically distributed so that on contraction the proboscis curls towards the concave surface. Each proboscis is supplied with a large nerve that originates in the cerebral ganglion and runs within the dorsal margin of the palps. There is also a large blood space. Palp pouches are features only found in the Nuculoidea. They are spoon-shaped and attached to the body at the point of attachment of the proboscis to the palp (Fig. 4). They establish continuity between the point of food collection and the distal oral groove of the palp. They have a simple structure consisting of two layers of cuboidal epithelium, separated by a thin layer of connective tissue. Within the latter is a material with similar staining properties to chitin. This material is also found in the gill plates where it forms the skeletal rods. Short cilia are present on the concave surface and margins of the pouch but not on the convex surface.

The gills are suspended obliquely from the postero-dorsal edge of the viscero-pedal mass across the posterior mantle cavity adjacent to the ventral margin of the posterior adductor muscle (Figs 3 & 4). The number of gill plates on the axis varies with the size of the specimen and ranges from 5 pairs in specimens ca. 1 mm in length to 24 pairs in mature specimens ca. 3 mm in length. Drew, (1901) found that 20 pairs was the common number in full grown specimens of the shallow-

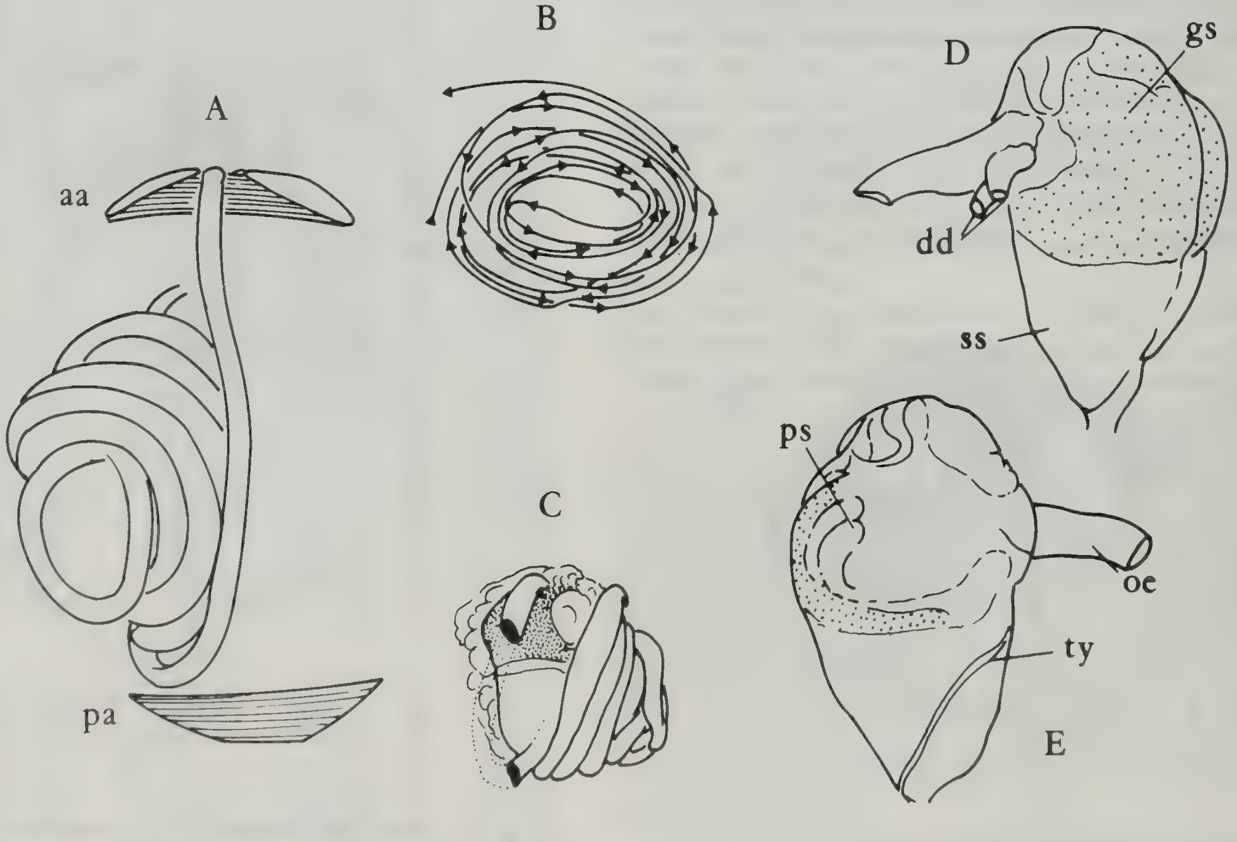

Fig. 6 *Deminucula atacellana*. A. Dorsal view of hind gut *in situ*; B. Course of hind gut as seen from right side—elucidated by dissection; C. Posterior view of stomach and hind gut—note a section of gut immediately posterior to the stomach is missing; D & E. Intact stomach as seen from the left and right side respectively. (Scale = 0.1 mm; for key abbreviations see p.63).

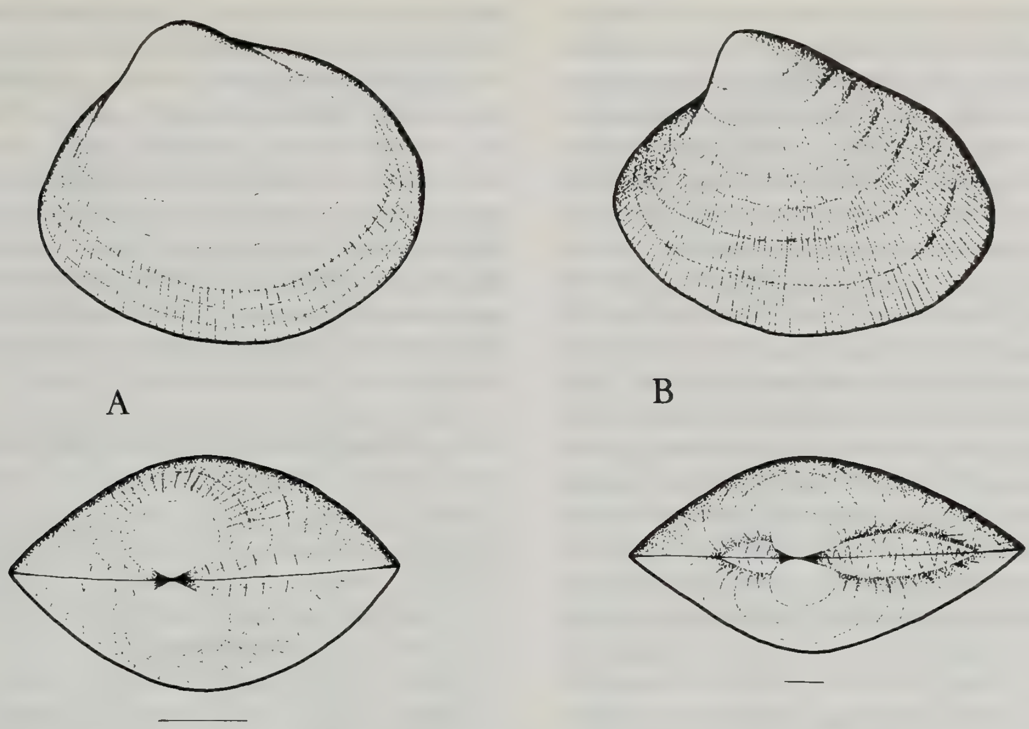

Fig. 7 A. *Deminucula atacellana* and B. *Nucula callicredemna*. A comparison of the external features of the two species as seen from right lateral and dorsal views. (Scales = 1.0 mm).

water species *Nucula delphinodonta* Mighels & Adams, 1842. The gill plates of *D. atacellana* have a different shape to those of *Nucula delphinodonta* (Figs 5a & b). In the latter case the plates are more triangular in shape. The finger-like plates of *D. atacellana* appear to be similar to those of *Nucula proxima*, another shallow-water species (Hampson, 1971), but when surface areas are compared, that of *D. atacellana* is less than half that of *N. proxima*. This may relate to the fact that deep-sea species have different respiratory requirements, but may also be a reflection of the small quantities of suspended material in deep water (Allen, 1978). Shallow-water species (eg. *N. nucleus*) may be facultative filter feeders (Caspers, 1940). The distal ends of the inner plates of each gill meet in the midline posterior to the foot. The gills of *D. atacellana* are supported by a skeletal framework, trichrome stain indicates that chitin occurs in the gill axis and in the ventral part of the gill plates. A few muscle fibres are present in the axis.

The nervous system of *D. atacellana* appears to be similar to that of *N. delphinodonta* (Drew, 1901). Cerebral ganglia are located on each side of the oesophagus and are connected by a short commissure that passes between the outer wall of the oesophagus and the anterior adductor muscle. From each cerebral ganglion there are two posteriorly directed commissures. The more dorsal passes through the viscera and joins with an elongate visceral ganglion anterior to the posterior adductor muscle. The ventral commissures extend into the foot to connect with the pedal ganglia. Adjacent and postero-dorsal to the pedal ganglia are a pair of statocysts which contain crystalline fragments, the statoliths. Cephalic sense organs (Vlès, 1905) are present on either side of the mouth close to the proximal palp ridge and immediately ventral to the cerebral ganglia and are innervated from the latter.

In *N. Nucleus* (Hirasaka, 1927) the cephalic sense organs comprise pigment cells with a cornea, in contrast to *D. atacellana* where there is a thickened epithelium which is innervated from the cephalic ganglia, but with no evidence of differentiation into cornea and pigment cells.

The hypobranchial gland (Pelseneer, 1891), consists of a layer of swollen columnar cells covering the surface of the suprabranchial cavity and the outer surface of the membrane suspending the gill axis (Fig. 5). The gland in *D. atacellana* is similar to that described for *Nucula delphinodonta* (Drew, 1901) and *Nucula turgida* (Yonge, 1939). According to Yonge, (1939) the function of the gland is to produce a secretion that binds any fine material which passes between the gill filaments into the suprabranchial cavity. In *Nucula delphinodonta* it has the additional function of forming a brood sac (Drew, 1901). Heath, (1937) believed that the gland produced different types of secretion in different species. In some species he found the gland stained deeply with Delafield's haematoxylin, whilst in others it remained unstained. In the case of *D. atacellana* different staining characteristics were found in different specimens. Sometimes it stained only with Orange G, sometimes with Aniline Blue, sometimes in part with Orange G and in part with Aniline Blue, and sometimes it would not take up any stain and remained colourless. The reasons for the apparent changing chemistry of this gland are unclear. Similarly the function of the gland is yet to be determined.

The foot has a similar shape and proportions to that of shallow-water species (Fig. 3). The sole is divided sagitally and there is a prominent heel. The margins of the sole are fringed with papillae. The number of papillae (c. 10) does not appear to vary with the size of the animal. A large, dorso-ventrally elongate, 'byssal' gland is present in the heel of the foot and from it a short duct opens at the posterior limit of the sole.

The pedal muscles of *N. delphinodonta* (Drew, 1901) are arranged in three pairs, two of which are attached antero-dorsally and the third postero-dorsally to the shell. The arrangement of *D. atacellana* differs from this and corresponds more closely with the arrangement in *Acila divaricata* (Heath, 1937). Thus, there is only one pair of anterior muscles lying immediately posterior to the oesophagus. Twin medial pedal muscles attach to each valve and then merge and pass to the outside of the stomach to serve the central region of the foot. There is a pair of posterior pedal muscles which pass to either side of the hindgut. In *Acila divaricata* the anterior pair are the largest, (Heath, 1937). This is not the case in *D. atacellana*, where all are approximately equal in size. The mechanics of foot movement in the protobranchs was described by Driscoll, (1964). The median and posterior pedal muscles are retractors, the anterior pair which control the anterior movement of the foot are protractors. Heath, (1937) believed that the posterior part of the anterior muscles also acted as a retractor. The 'byssal' gland in the heel of the foot of protobranchs opens to the median groove of the foot, however, nothing comparable to byssus threads have been observed. Its structure differs greatly from the byssus gland of lamellibranchs and there is no evidence that it is a vestige of a post-larval gland (Heath, 1937). In the protobranchs it varies greatly in size in different species although it is fairly consistent in its composite structure. In *D. atacellana* it is comparatively large. The lumen of the gland may contain traces of a secretory material. The surrounding cells are usually swollen and vacuolated.

In general the form of the gut of *D. atacellana* compares well with descriptions given by Yonge, (1939) and Owen, (1956) for shallow-water species. The mouth is situated mid-ventrally a short distance behind the anterior adductor muscle (Fig. 3). At the point of its junction with the distal oral grooves it is laterally distended and bilobed in cross-section. The oesophagus enters the stomach antero-dorsally and a little to the left of the mid-line. This is in contrast to *Nucula sulcata* where the oesophagus enters the stomach to the right of the mid-line (Owen, 1956), however, in *D. atacellana* most of the right side of the body is occupied by the extremely elongate hindgut (see below). The oesophageal epithelium is much folded and is made up of a mixture of cuboid and columnar cells. The epithelial cells are richly ciliated and there are mucous cells present between them. There is a layer of subepithelial circular muscle that is progressively thicker towards the stomach, so much so that it probably forms a sphincter at the junction with the stomach. Functionally this is essential to prevent regurgitation of the stomach contents when under pressure.

The combined stomach and style sac consist of a dorsal globular region—the stomach proper—and a ventral conical tapering style sac (Fig. 6). The dorsal hood ('dorsal pouch' of Graham, 1949) extends along the left wall of the stomach to end blindly on the left dorsal side. As in most protobranchs three ducts enter the stomach anteriorly from the digestive diverticula. In *D. atacellana* there is one on the left and two adjacent to each other close to the mid-line and ventral to the oesophagus. There is no small caecum similar to that found on the right of the mid-dorsal line in the stomach of *N. sulcata* (Owen, 1956). A grooved ciliated sorting area which extends over most of the right side of the stomach is visible through the stomach wall. In a specimen approximately 3 mm long seven grooves are present. This compares with more than 25 in a specimen of *N. sulcata* 15 mm in length. A reduction in the number of the ciliated grooves is a consistent feature in deep-sea species. The left wall of the stomach is lined with a gastric shield and in the region of the dorsal hood this is thickened to form a pronounced tooth. Previously regarded simply as an inert structure serving to protect the underlying epithelium and assist in the trituration of the gastric contents, Halton & Owen, (1968) showed it has a far more elaborate structure and function. There are two components, an inner part consisting of numerous microvilli of underlying epithelial cells which extend into the secreted matrix and, an outer matrix of non-cellular chitin. At intervals on certain microvilli vescicular swellings are present. Histochemical studies show the shield to be enzymatically active. The epithelium underlying the shield is of columnar cells which are tallest in the region of the gastric tooth. Distally these cells are packed with pigment granules. Yonge, (1939) and Owen, (1956) suggest that they are probably excretory. Histochemical studies suggest they are related to lipofuschin pigments which are generally regarded as by-products of lipid metabolism. Underlying the epithelium of the stomach is a layer of collagen and a system of muscle fibres.

The hindgut is extremely long. This is characteristic of deep-sea nuculids and it is particularly elongate in *D. atacellana* (fig. 6). This may relate to the fact that deep-sea sediments make a poor diet with many of the organics resistant to digestion and therefore demanding of time for digestion, however, the discovery of complete forameniferans in the stomach perhaps indicate more *living* matter is ingested than was previously thought.

Heath, (1937) used the configuration of the hindgut as a diagnostic feature and found the simplest and possibly the most-primitive nuculoid configuration is that found in species of *Acila*. The more-complex extensive overlapping of the coils in *D. atacellana* makes the course of the gut difficult to determine except by three dimensional reconstruction (Fig. 6).

The digestive diverticula of *D. atacellana* consist of numerous blind-ending tubules which communicate with the stomach by a system of unbranched secondary ducts and much-branched main ducts. The main ducts are lined with cuboidal cells with a spherical or slightly oval nucleus and numerous pigmented cytoplasmic granules. Owen, (1956) in studies on living *N. sulcata* found these latter to be lipo-pigments staining strongly with Sudan Black B, suggesting that they were a bi-product of lipid metabolism and, from frozen sections, he confirmed the presence of lipids in the basal region. The cells are without cilia but have a well-developed brush border.

Secondary ducts in *D. atacellana* are similar to main ducts. This is in contrast to *N. sulcata* where secondary ducts have a dense coat of long cilia which extend almost to the centre of the lumen. While individual tubules of *N. sulcata* are round or oval in cross-section (Owen, 1956), those in *D. atacellana* are much more irregular. This appears to be a consistent feature in deep-sea protobranchs. Two types of cell occur. The most numerous have an irregular outline and are highly vacuolated. They contain two types of cytoplasmic granule, one large and blue staining and the other small and usually red in trichrome staining. The blue colour indicates an external membrane of basophilic mucus, the red colour indicates an acid mucopolysaccharide. A second, much less common, type of cell is present in small clusters scattered within the tubules. They are distinguishable by a lack of granules, a more-prominent nucleus and a more-darkly staining cytoplasm. They tend to be triangular in outline and distally narrow. According to Owen, (1956), they possess a single flagellum but this was not seen in *D. atacellana*. The dark staining cells have been regarded as excretory and secretory, but it remains unclear what function they perform (Owen, 1956). No evidence of intra-cellular digestion was seen and it is generally agreed that digestion in protobranchs is exclusively extra-cellular.

Studies of *D. atacellana* by Sanders and Hessler, (1969), Scheltema, (1972) and Grassle & Sanders, (1973) from the North America Basin suggests this species has non-periodic reproduction. Preliminary evidence from samples taken in February, June, October and November from Biscay supports this view.

Sexes are separate and of equal proportions. Gonads are simple, paired, and overlie the viscera. The gonoducts open into the supra-branchial cavity. Maximum diameter of the ova is 135 µm. Approximately 200 ova are present in a specimen 3.3 mm total length. No brooding of the eggs occurs, development is probably lecithotrophic (Scheltema, 1972).

COMPARATIVE SHELL MEASUREMENTS OF SPECIMENS OF *D. atacellana*

Dimension (mm)	No.	Mean	SD	Max.	Min.
		NORTH AMERICA BASIN			
Length	45	3.07	0.88	5.04	1.51
Width		1.88	0.57	3.23	0.94
Height		2.71	0.79	4.55	1.34
		WEST EUROPEAN BASIN			
Length	77	2.96	1.14	4.87	0.78
Width		1.85	0.75	2.89	0.48
Height		2.58	0.96	4.02	0.76
		BAY OF BISCAY			
Length	134	2.68	0.84	4.53	0.69
Width		1.67	0.56	2.96	0.45
Height		2.34	0.72	3.75	0.68
		S.E. ATLANTIC			
Length	58	2.46	1.57	5.54	0.84
Width		1.42	0.93	3.33	0.45
Height		2.17	1.37	4.77	0.76
		GUYANA BASIN			
Length	17	3.67	1.74	6.50	1.34
Width		2.04	0.99	3.75	0.75
Height		3.13	1.49	5.50	1.16
		CANARIES BASIN			
Length	14	1.77	0.42	2.78	1.37
Height		1.05	0.24	1.64	0.83
Height		1.56	0.34	2.41	1.23
		CAPE VERDE BASIN			
Length	7	2.26	0.73	3.49	1.46
Width		1.30	0.44	2.10	0.88
Height		1.95	0.60	2.92	1.29
		ARGENTINE BASIN			
Length	23	3.50	1.10	5.20	1.14
Width		1.96	0.64	3.11	0.66
Height		3.18	1.00	4.74	1.05

DISTRIBUTION

D. atacellana is common and widespread. The species was originally described from specimens taken from the West European Basin by Jeffreys, (1881). It also was recorded from the North America Basin (Verrill, 1884), the Surinam Basin (Dall, 1890) and the Canaries Basin (Dautzenberg and Fischer, 1897). The species occurs throughout the North Atlantic, as far north as the Rockall Trough in the east and the Davis Strait in the west. In the South Atlantic it occurs in the Guinea, Angola and Argentine Basins but to date has not been taken from the Brazil Basin or the Sierra Leone Basin nor is it recorded by Clarke, (1961) in the Cape Basin. It appears to be absent from high latitudes—the Antarctic (Thiele, 1912; Dell, 1972), Arctic (Clarke, 1960; Bernard, 1979) and Norwegian Basins (Bouchet & Warén, 1979).

D. atacellana is the most eurybathic of the deep-sea nuculids with a vertical range of approximately 4000 m. It is not found in depths less than 1000 m. Shallow-water nuculids appear not to occur much beyond the continental shelf edge eg. Thus for European seas with the possible exception of *Nuculoma tenuis* and *Nucula tumidula* Malm shelf species which penetrate down slope to some degree, there appears to be little overlap of shelf and slope species at the extremities of their ranges. More sampling will be necessary to confirm this but there appears to be a gap between 200 m and 500 m in which few species of *Nucula* dominate. *D. atacellana* consistently occurs deeper in the Basins south of the equator than in the north. This may possibly relate to the absence of *Brevinucula verrilli* (p. 85) from the southern Basins.

Nucula callicredemna Dall, 1890

Figs 7b & 8

TYPE LOCALITY: Albatross Sta. 2754, Northeast of Tobago, Lat. 11°40′N., Long. 58°33′W, 1609 m.

TYPE SPECIMEN: Holotype. No holotype was designated. The type lot (USNM–95431) contained 11 valves, 1 conjoined specimen and several fragments (James, 1972). Re-examined (1991, JAA) 6 valves (4 in poor condition) and one conjoined specimen and fragments. Conjoined specimen selected as lectotype.

Nucula callicredemna Dall 1890, p. 258, pl. 31, Fig. 9; James 1972, p. 29, 34–36, Figs 5–14, map 2.

Nucula crenulata var. obliterata Dall 1886 p. 247, (in part); (*non N. crenulata var. obliterata* Dall, 1881).

Nucula obliterata Knudsen, 1970, p. 177; Pequegnat, 1972, p. 74.

Nucula aureliae Métivier, 1982, p. 39–42, Fig. 1, pl. 1, Figs 1–2.

DEPTH RANGE: 3411–4077 metres.

The taxonomy of this species is complicated by the fact that Dall, (1886) incorrectly identified a specimen of *N. callicredemna* (USNM. 63133) from 'Blake' Sta. 236 as *Nucula crenulata var. obliterata* (Knudsen, 1970). It is also possible that certain specimens in past records reported as *N. cancellata* (= *D. atacellana*) could be small specimens of *N. callicredemna* (p. 66). We believe that *Nucula aureliae* which Métivier, (1982) has described from 3360 metres off the Azores Archipeligo is synonymous with *N. callicredemna* and, if true, its range is now extended to the Canaries Basin. Métivier, (1982) who regarded *N. aureliae* as being similar to *N. cancellata* (= *D. atacellana*) failed to mention *N. callicredemna. N. callicredemna* also appears to be identical, certainly in shell morphology, to the Arctic deep-sea species *Nucula zophos* (Clarke, 1960), although this cannot be certain until the internal morphologies have been compared. Dall, (1890) also regarded *N. callicredemna* as being similar to the Pacific deep-sea species *Nucula niponica* (Smith, 1885).

N. callicredemna originally taken from off Tobago in 1609 metres (Dall, 1890) is now known to be common in the Gulf of Mexico in depths ranging from 2122 metres to 3563 metres (James, 1972). The one specimen taken off Recife in the Brazil Basin now extends the range of the species approximately 2180 km south.

MATERIAL

Cruise	Sta	Depth (m)	No	Lat	Long	Gear	Date
			BRAZIL BASIN				
Atlantis II	156	3459	1	00°46.0'S	29°28.0'W	ES	14.02.67
			GUYANA BASIN				
Knorr	306	3392	4	09°31.1'N	56°20.6'W	ES	02.03.72
			VENEZUELA BASIN				
Norda	33	3800–4035	1	15°08.0'N	69°12.0'W	OT	24.10.81
	35	3954–4017	16	15°08.0'N	69°12.0'W	OT	25.10.81
	36	3951–4044	24	15°08.0'N	69°12.0'W	OT	26.10.82
	37	3995–4097	11	15°08.0'N	69°12.0'W	OT	27.10.81
	38	3995–4013	15	15°08.0'N	69°12.0'W	OT	28.10.81
	39	3993–4065	1	15°08.0'N	69°12.0'W	OT	28.10.81
	40	3967–4009	11	15°08.0'N	69°12.0'W	OT	28.10.81
	87	3482–3518	22	13°30.0'N	64°45.0'W	OT	25.11.81
	88	3516–3550	25	13°30.0'N	64°45.0'W	OT	25–26.11.81
	90	3422–3464	19	13°30.0'N	64°45.0'W	OT	26–27.11.81
	91	3459–3503	12	13°30.0'N	64°45.0'W	OT	27.11.81
	92	3476–3518	34	13°30.0'N	64°45.0'W	OT	27–28.11.81
	93	3411–3459	21	13°30.0'N	64°45.0'W	OT	28.11.81
	94	3428–3476	11	13°30.0'N	64°45.0'W	OT	28–29.11.81

SHELL DESCRIPTION

The original shell description by Dall, (1890) is detailed, although as pointed out by James, (1972) it is in reverse ie. in the description anterior is posterior and *vice versa*. A summary description is given here.

Shell large, ovoid, lustrous, equivalve, inequilateral, surface covered in fine concentric ridges, radial striations give surface a fine reticulated appearance; umbos (frequently eroded) posterior to the midline, opisthogyrate; when posterior margin orientated vertically the anterior dorsal margin is above the horizontal; lunule long, escutcheon short and broad, dentition often visible dorsally through the shell, especially beneath the lunule; resilifer oblique to narrow hinge plate, extends ventral to anterior proximal teeth, teeth typically chevron-shaped but obtusely angled, number varies with the size of the specimen (6 posterior and 8 anterior teeth in a specimen 3.1 mm in length and 15 posterior and 29 anterior teeth in a specimen 18.9 mm in length (James, 1972), ligament tear-drop shaped.

Nucula callicredemna: MEASUREMENTS (FROM JAMES, 1972)

Sta.	V	L	H	B	A	P
6813–9	l	18.9	14.0	3.6	29	15
‘	r	18.9	14.0	3.5	30	14
6787–4A	l	12.2	9.4	3.2	21	11
‘	r	12.2	9.4	3.2	21	11
‘	l	9.2	7.7	2.2	19	10
‘	r	9.2	7.7	2.2	19	10
65A14–6	l	6.1	5.2	1.4	14	7
‘	r	6.1	5.2	1.4	13	7
‘	l	3.1	3.0	0.9	10	6
‘	r	3.1	3.0	0.9	8	6

V = valve, r = right valve, l = left valve, L = length (mm), H = height (mm), B = breadth (mm), A = number of anterior teeth, P = number of posterior teeth.

Characteristically, *N. callicredemna* has a well-developed chondrophore that extends ventral to the anterior proximal teeth and is similar to that in shallow-water species such as *Nucula sulcata* (Fig. 8). It has similar proportions to that of many shelf species but the large size of the shell (19 mm total length), is unusual in a deep-sea species (James, 1972). It is by far the largest deep-sea nuculid in the Atlantic.

INTERNAL MORPHOLOGY

Discounting differences related to size the internal morphology is not greatly different from that of *D. atacellana*. The palp is large and deep covering much of the foot and in a specimen 16 mm total length there are 65–70 palp ridges. The gill is narrow lying diagonally across the posterior part of the mantle cavity. The axis is parallel to the postero-dorsal shell margin. The same specimen bears 32 gill plates. The course of the hind gut is similar to that of *D. atacellana*. There are fourteen ridges on the posterior sorting area of the stomach.

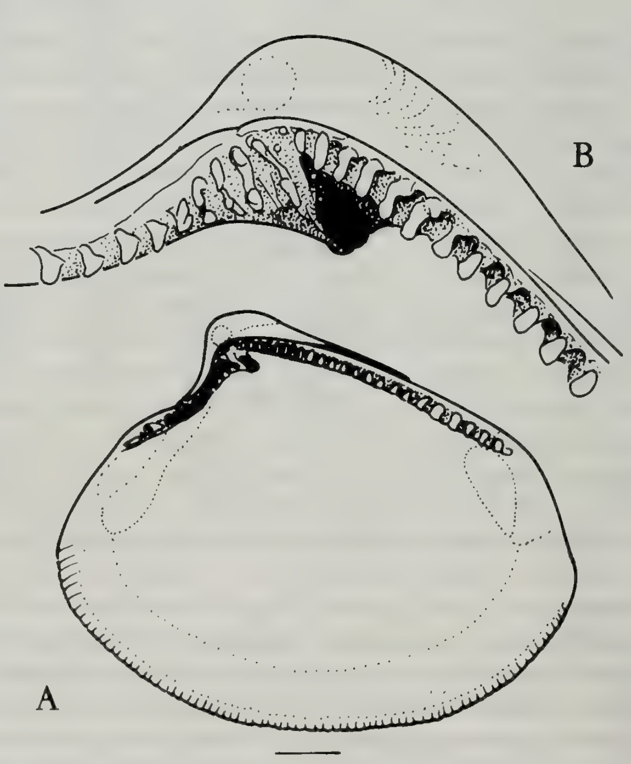

Fig. 8 *Nucula callicredemna*. A. Internal view of left valve; from Station 156; B. Detail of hinge of same valve. (Scales = 1.0 mm).

Nuculoidea bushae (Dollfuss, 1898)

Figs 9–11

TYPE LOCALITY: U.S. Bureau Fisheries Sta. 2171, Lat. 37°59′30″N, Long. 73°48′40″W.

TYPE SPECIMEN: Holotype: USNM No. 40474.

Nucula subovata Verrill & Bush, 1898, p. 858, pl. 81, Fig. 8; pl. 83, fig. 5; Johnson, 1934, p. 15; (*non* D'Orbigny, 1850).
Nucula bushi Dollfuss, 1898, p. 180.
Nucula bushae emend Schenck, 1939, p. 37.

DEPTH RANGE: 509–2876 metres.

MATERIAL

Cruise	Sta	Depth (mm)	No	Lat	Long	Gear	Date
			NORTH AMERICA BASIN				
Atlantis	D1	509	13	39°54.5′N	70°35.0′W	AD	23.05.62
Chain	105	530	235	39°56.6′N	71°03.6′W	ES	05.05.66
			WEST EUROPEAN BASIN				
Sarsia	S44	1739	67	43°40.8′N	30°35.2′W	ES	16.07.67
	S65	1922	1	46°16.5′N	04°44.0′W	ES	25.07.67
Chain	313	1500	46	51°32.2′N	12°35.9′W	ES	17.08.72
Chain	314	1015	42	51°54.6′N	12°27.3′W	ES	18.08.72
	316	2209	10	50°58.7′N	13°01.6′W	ES	18.08.72
Challenger	4	1993	85	56°52.0′N	10°01.0′W	ES	05.06.73
	12	2076	19	56°49.0′N	10°15.0′W	ES	20.09.73
	13	1842	93	56°45.0′N	09°50.0′W	ABD	22.09.73
	15	1632	32	56°44.0′N	09°28.0′W	ES	22.09.73
	18	1392	64	56°44.0′N	09°20.0′W	ES	22.09.73
	20	1271	336	56°46.0′N	09°17.0′W	ES	23.09.73
	22	1028	392	56°41.0′N	09°11.0′W	ES	23.09.73
	61	2000	1	57°08.0′N	12°09.0′W	SBC	23.06.76
	63	1800	6	56°37.0′N	09°49.0′W	SBC	25.06.76
	64	1400	2	56°39.0′N	09°29.0′W	SBC	26.06.76
	65	1600	5	56°39.0′N	09°40.0′W	SBC	26.06.76
	66	1200	2	56°39.0′N	09°23.0′W	SBC	26.06.76
	67	1000	1	56°39.0′N	09°13.0′W	SBC	26.06.76
	68	1800	2	58°42.0′N	09°43.0′W	SBC	01.07.76
	99	1160	264	60°00.0′N	10°35.0′W	ES	09.07.76
	105	1600	15	58°27.0′N	12°35.0′W	ES	10.07.76
	155	1330	6	48°27.0′N	10°20.0′W	SBC	04.08.79
	156	1310	6	48°27.0′N	10°21.0′W	SBC	05.08.79
	159	2036	3	50°55.0′N	12°21.0′W	SBC	08.08.79
	188	2876	1	54°40.6′N	12°16.1′W	SBC	15.08.81
	215	2001	2	57°02.0′N	09°47.0′W	SBC	03.08.82
	220	1608	8	59°05.0′N	08°51.0′W	SBC	04.08.82
	222	1101	15	59°43.0′N	07°43.0′W	SBC	05.08.82
	232	2105	8	57°17.0′N	10°16.0′W	ES	19.05.83
	272	2250	1	56°40.0′N	10°30.0′W	SBC	05.08.83
	273	2185	10	56°05.0′N	10°28.0′W	AT	05.08.83
	277	1593	1	56°16.0′N	09°44.0′W	SBC	06.08.83
Incal	DS02	2081	1	57°58.8′N	10°48.5′W	SD	16.07.76
	CP02	2091	3	57°58.4′N	10°42.8′W	SD	16.07.76
			BAY OF BISCAY				
Biogas I	DS11	2205	1	47°35.5′N	08°33.7′W	SD	08.08.72
Biogas III	DS49	1845	20	44°05.9′N	04°15.6′W	SD	01.09.73
	DS50	2124	3	44°08.9′N	04°15.9′W	SD	01.09.73
Biogas IV	DS52	2006	24	44°06.3′N	04°22.4′W	SD	18.02.74
Biogas V	CP07	2170	7	44°09.8′N	04°16.4′W	CP	21.06.74
Biogas VI	DS71	2194	1	47°34.3′N	08°33.8′W	SD	20.10.74
	CP24	1995	5	44°08.1′N	04°16.2′W	CP	31.10.74
DS86		1950	9	44°04.8′N	04°18.7′W	SD	31.10.74
	DS87	1913	14	44°05.1′N	04°19.4′W	SD	01.11.74
	DS88	1894	14	44°05.2′N	04°15.7′W	SD	01.11.74
Polygas	DS18	2138	1	47°32.9′N	08°44.9′W	SD	22.10.72
	DS25	2094	11	44°08.2′N	04°15.7′W	SD	01.11.72
	DS26	2076	11	44°08.2′N	04°15.0′W	SD	01.11.72
			GUYANA BASIN				
Knorr	295	1022	28	08°04.2′N	54°21.3′W	ES	28.02.72
			GUINEA BASIN				
Walda	DS28	1261	37	04°21.2′N	04°35.2′E	SD	00.00.71
			ANGOLA BASIN				
Atlantis II	203	542	22	08°48.0′S	12°52.0′E	ES	23.05.68
			CANARIES BASIN				
Discovery	6696	1780	3	28°06.0′N	13°28.0′W	ES	15.03.68
	6697	1564	2	17°57.0′N	13°46.2′W	ES	15.03.68
	6701	1934	12	27°45.2′N	14°13.0′W	ES	16.03.68
	6704	2129	17	27°44.9′N	14°25.0′W	ES	17.03.68
			CAPE VERDE BASIN				
Atlantic II	138	1976	30	10°36.0′N	17°52.0′W	ES	04.02.67
	139	2187	21	10°33.0′N	17°53.0′W	ES	04.02.67
	141	1796	38	10°30.0′N	17°51.5′W	ES	05.02.67
	142	1796	101	10°30.0′N	17°51.5′W	ES	05.02.67
	143	2095	18	10°35.0′N	17°44.0′W	ES	05.02.67
	144	2357	39	10°36.0′N	17°40.0′W	ES	05.02.67
	145	2185	25	10°36.0′N	17°49.0′W	ES	06.02.67

A closely related species appears to be *Nucula aegeensis* Forbes, (1844). Like many Forbes types, that of *N. aegeensis* has been lost, and although specimens named *N. aegeensis* exist and have been examined, eg. Jeffreys collections in the BM(NH) No. 85.11.5.560–4 and 85.11.5.567–570 and USNM, there is no certainty that these are in fact the species that Forbes described from off Crete. Indeed Jeffreys, (1879) is uncertain and states "Assuming this to be Forbes's species (although his description is too scanty to be satisfactory)."

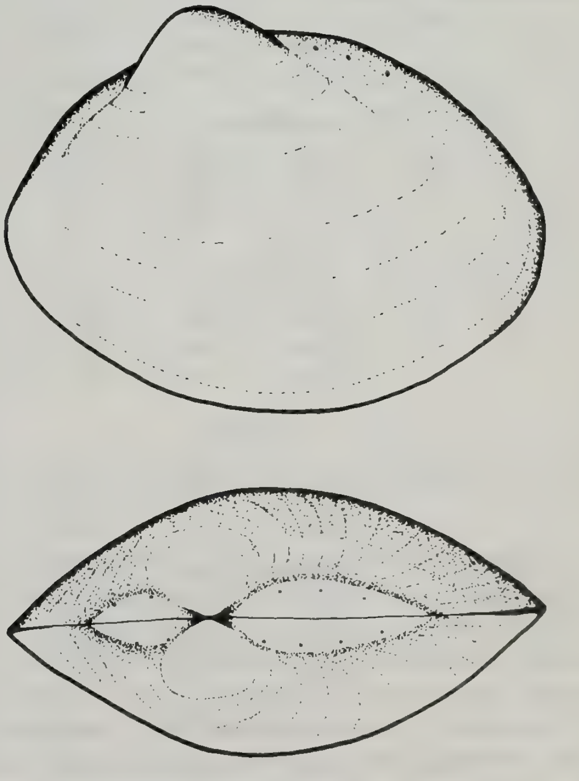

Fig. 9 *Nuculoidea bushae*. Lateral and dorsal views of a shell from Station 87. (Scale = 1.0 mm).

Specimens of Jeffreys labelled *N. aegeensis* differ markedly in shape and fringe detail from *N. bushae*. Likewise Dall, (1886) also identified *N. aegeensis* from the Atlantic off Havana in 320 m and 823 m, off Morro Light 479 m and off St Vincent in 847 m regarding this as a geographical race of *Nuculoma tenuis* a view not supported by Jeffreys, (1879). There is certainly confusion, an easily accessible example is a comparison of the photograph in Abbott, (1974) of a West Atlantic specimen against a well-figured specimen in Locard, (1898). They are dissimilar in details of hinge and outline.

SHELL DESCRIPTION

The description by Verrill & Bush, (1898) is detailed and accurate.

Shell small, elongate-ovate, equivalve, inequilateral; semi-transparent, dentition often visible through shell, surface smooth, lustrous with fine concentric lines; umbos posterior to midline, orthogyrate, to slightly opisthogyrate; when posterior margin orientated vertically anterior dorsal margin is well above the horizontal; lunule often bordered by tiny perforations, escutcheon indistinct; teeth typical chevron-shape, number varying with size of specimen, 3 posterior and 4 anterior teeth in a specimen 1.64 mm in length and 6 posterior and 9 anterior teeth in a specimen 4.47 mm in length, ligament slightly oblique to moderately narrow hinge plate, does not extend ventral to anterior proximal teeth.

COMPARATIVE SHELL MEASUREMENTS OF *Nuculoidea bushae*

Dimension (mm)	No	Mean	SD	Max	Min
		NORTH AMERICA BASIN			
Length	25	2.70	1.05	4.78	1.05
Width		1.23	0.479	2.28	0.53
Height		2.01	0.764	3.51	0.82
		WEST EUROPEAN BASIN			
Length	23	2.05	0.75	4.11	0.86
Width		1.06	0.35	2.13	0.49
Height		1.64	0.55	3.26	0.60
		BAY OF BISCAY			
Length	54	2.68	0.85	3.99	1.25
Width		1.44	0.51	2.36	0.68
Height		2.13	0.69	3.14	1.01
		ANGOLA BASIN			
Length	55	2.23	0.95	5.91	0.73
Width		1.00	0.45	2.67	0.35
Height		1.72	0.72	4.38	0.59
		GUYANA BASIN			
Length	28	1.18	0.46	2.54	0.76
Width		0.57	0.19	1.03	0.400
Height		0.92	0.33	1.82	0.61
		CANARIES BASIN			
Length	5	3.24	0.99	3.85	1.47
Width		1.83	0.57	2.22	0.83
Height		2.65	0.818	3.17	1.21
		CAPE VERDE BASIN			
Length	29	2.82	0.76	3.92	1.34
Width		1.46	0.44	2.15	0.73
Height		2.22	0.50	2.93	1.09

INTERNAL MORPHOLOGY

N. bushae differs from *Deminucula atacellana* in having a much more extensive foot with less pronounced papillae but with a marked heel. The 'byssal' gland is large. In *N. bushae* the adductor muscles are oval in cross-section and the anterior is slightly larger than the posterior. The 'quick' and 'catch' portions are approximately equal in size. The gill axis lies parallel to the postero-dorsal margin of the shell. The gill plates number 30 in a specimen 3.1 mm in length. The palps are relatively large compared with *D. atacellana* but do not extend beyond the limits of the foot. The palp ridges number 30 in a specimen ca. 2 mm in length. The palp proboscides, although highly contracted, appear to have the same relative proportions as in *D. atacellana*. The stomach differs from that of *D. atacellana* in being more slender and the hind gut is less extensive (Fig. 11). The maximum recorded diameter of ova from these samples is 140 μm. This is in contrast to Scheltema (1972) who recorded an egg diameter of 270 μm. We believe that this is because Scheltema (1972) had examined specimens of *N. similis* a species of very similar appearance. There is no evidence of seasonal reproduction and fully mature specimens were recorded in February, June, August and October.

DISTRIBUTION

Nuculoidea bushae occurs in the North America, Angola, Guinea, Guyana, Canaries, Cape Verde and West European Basin, the latter includes the Rockall Trough and the Bay of Biscay. Verrill & Bush, (1898) thought that *Nuculoidea bushae* to be closely related to the shallow water species *Nuculoma tenuis*. The shell is, however, much less oblique and more elongate than in the latter species, while the hinge plate of *N. bushae* is broader and the resilifer is more rounded, less oblique and does not extend ventral to the anterior teeth. Verrill & Bush, (1898) collected *N. bushae* from four U.S. Fisheries Commission stations in the North American Basin between Lat. 40°00.0′N. Long. 71°14′30″W, and Lat. 37°8′N, Long. 74°33′W., in 287–812 m but, until now, the species has not been recorded from other regions of the Atlantic.

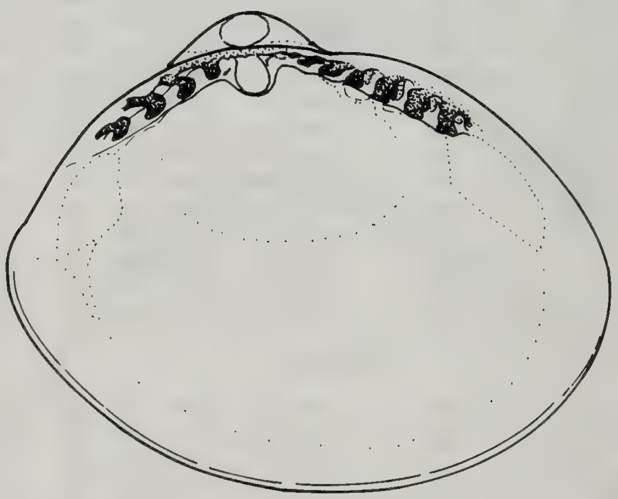

Fig. 10 *Nuculoidea bushae*. Internal view of left valve from Station 314. (Scale = 1.0 mm).

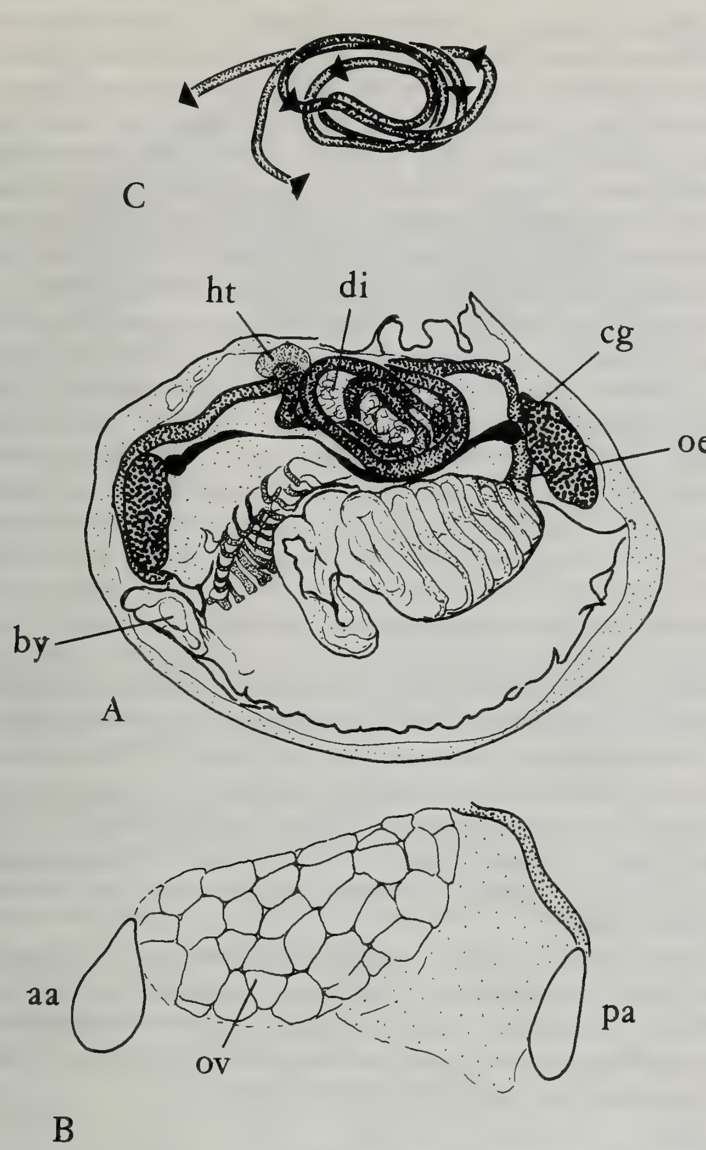

Fig. 11 *Nuculoidea bushae*. A. Semidiagrammatic view from the right side of the body organs; B. Lateral view of part of body from the left side to show the position of the ovary in a mature specimen; C. Course of hind gut as seen from the right side. (Scale = 1.0 mm; for key to abbreviations see p.63).

Nuculoidea pernambucensis (Smith 1885)

Figs 12–14

TYPE LOCALITY: Challenger Sta. 120, Lat. 08°37′00″S, Long. 34°28′00″W, 675 fms.

TYPE SPECIMENS: Syntypes, 5 valves, BM(NH) reg.no. 1887.2.9.2910–11. (Examined by PR). (Note: Two specimens from Knorr, Sta. 293, 08°58.0′N, 54°04.3′W, 1518 m lodged in BM(NH) No. 1990012).

Nucula pernambucensis Smith, 1885, p. 227, pl. 18, Figs 10–10a.
Nucula cymella Dall, 1886, p. 246; 1889, p. 42; 1890, p. 258, pl. 13, Fig. 1; 1903, p. 42; Johnson, 1934, p. 16; Clarke, 1962, p. 48; Knudsen 1970, p. 220.
Nucula turnerae Clarke, 1961, p. 367, 368; pl. 2, Figs 2, 3; 1962, p. 49.

DEPTH RANGE: 587–2976 metres.

Nucula cymella Dall, (1890) was synonymized with *Nuculoidea pernambucensis* by James, (1972). Clarke, (1960) noted that *Nucula turnerae* from the Argentine Basin was similar to *Nuculoidea pernambucensis* and that it was possibly a juvenile specimen of the latter species. Verrill & Bush, (1898) also noted *Nuculoidea bushae* resembled both *Nuculoidea pernambucensis* and *Nuculoma tenuis*. *N. pernambucensis* appears to be closely related and probably congeneric with *Nucula* sp. A described by James, (1972) from the Gulf of Mexico.

MATERIAL

Cruise	Sta	Depth (m)	No	Lat	Long	Gear	Date
				GUYANA BASIN			
Knorr	293	1518	23	08°58.0′N	54°04.3′W	ES	27.02.72
	299	2076	3	07°55.1′N	55°42.0′W	ES	29.02.72
				BRAZIL BASIN			
Atlantis II	167	975	4	07°58.0′S	34°17.0′W	ES	20.02.67
	169	587	12	08°03.0′S	34°23.0′W	ES	21.01.67

SHELL DESCRIPTION

The original description by Smith, (1885) is not very detailed.

Shell broadly ovate, somewhat triangular, equivalve, inequilateral, transluscent, with dentition often visible through shell, strong concentric ridges; umbos posterior to the midline, orthogyrate; when postero-dorsal margin orientated vertically antero-dorsal margin well above horizontal; lunule often bordered by tiny perforations, escutcheon indistinct; hinge-teeth, small, pustular, 3 posterior and 4 anterior teeth in specimen of 1.97 mm in length, and 9 posterior and 11 anterior teeth in specimen 5.70 mm in length, ligament perpendicular to very broad hinge plate, does not extend ventral to anterior proximal teeth.

COMPARATIVE SHELL MEASUREMENTS OF *Nuculoidea pernambucensis*

Dimension (mm)	No	Mean	SD	Max	Min
		GUYANA BASIN			
Length	19	3.69	0.85	5.06	1.97
Width		2.00	0.54	3.02	0.97
Height		2.99	0.69	4.06	1.56
		BRAZIL BASIN			
Length	9	3.92	0.73	5.70	3.25
Width		2.17	0.57	3.54	1.64
Height		3.26	0.63	4.73	2.60

N. pernambucensis appears to be unique among extant nuculids in possessing an extremely broad hinge plate with narrow obtuse and somewhat pustulate teeth (Fig. 12). This feature is fairly common among Palaeozoic species, for example species of *Tancrediopsis* Beushausen (McAlester, 1963; Bradshaw, 1970) and *Nuculoidea* Williams & Breger (Vokes, 1949). This type of hinge is also present in an unusual nuculoid *Tironucula jugata* from the Lower Ordovician of Spitzbergen (Morris & Fortey, 1976). This latter species originally placed in a family Praenuculidae (McAlester, 1969) was later regarded by Morris & Fortey, (1976), on the basis of

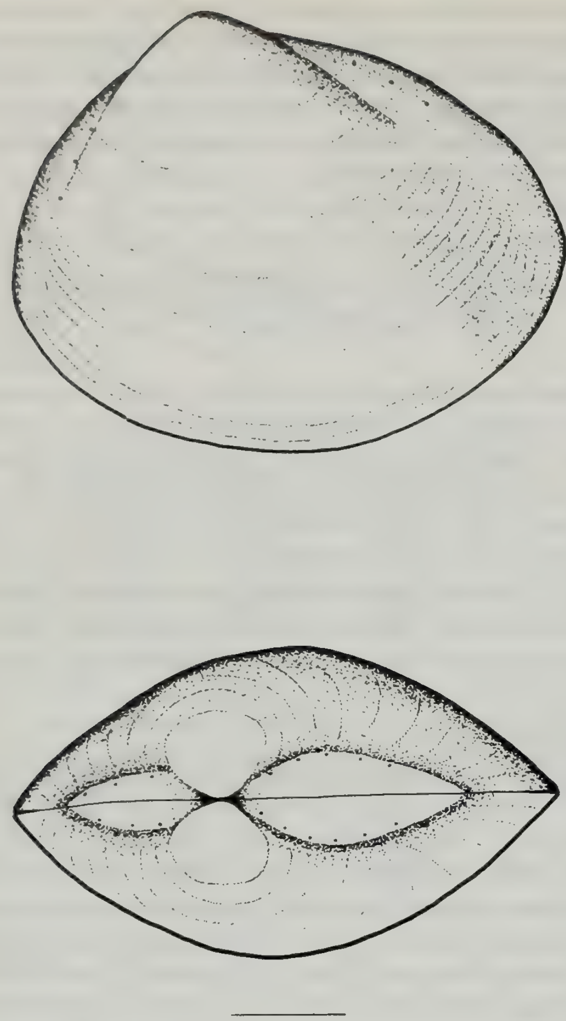

Fig. 12 *Nuculoidea pernambucensis*. Lateral and dorsal views of a shell from Station 293. (Scale = 1.0 mm).

its hinge morphology, as intermediate between taxodont and actinodont forms. Actinodont dentition is probably the more primitive and gave rise to the taxodont condition. Allen & Sanders, (1973) point out that the lack of taxodont teeth *per se* can no longer be used as the prime criterion for excluding fossil bivalves from the Nuculoidea. *N. pernambucensis* also resembles the Silurian fossil *Nuculoidea pinguis pinguis* (Soot-Ryen, 1964); *N.p. pinguis* together with members of the primitive nuculoid family Ctenodontidae, are thought by Soot-Ryen, (1964) to have lived in a deep-sea environment. This is based on the fact that they lived in muddy sediments so tranquil that valves did not separate after the animal's death.

INTERNAL MORPHOLOGY

The adductor muscles are oval, the anterior being slightly larger than the posterior. The 'quick' and 'catch' portions are approximately equal in size. The gill axis lies parallel to the posterior dorsal margin of the shell and gill plates number 20 in a specimen 3.9 mm in length. The palps are relatively longer than those of *D. atacellana* and palp ridges number 40 in a specimen 4 mm in length. The 'byssal' gland is large.

DISTRIBUTION

Because only dead valves had been collected from abyssal depths Knudsen, (1970) did not regard *Nuculoidea pernambucensis* as truly abyssal, and James, (1972) on the basis of collections from the Gulf of Mexico, also supported this view. The results here confirm that it occurs at abyssal depths at least in the Guyana Basin.

HMS 'Challenger' originally collected *N. pernambucensis* off Pernambuco (Recife) on the slope of the Brazil Basin. *Nucula cymella* was recorded from the Yucatan Straits, Florida Strait, south of Cuba, east of Tobago and north of Ceara, Brazil (Dall, 1890) and *N. turnerae* was collected in the Argentine Basin at 'Vema' Sta. 12 (Clarke, 1961). James, (1972) collected *N. pernambucensis* in the north east and the north west of the Gulf of Mexico at depths of 732–1683 m but living specimens were only taken in depths of 1000–1494 m.

Since specimens are found at upper slope depths it is possible that *N. pernambucensis* may have evolved following a downward migration of an adjacent shelf species of the tropical shelf of South America and/or the Gulf of Mexico. Such a theory may explain why this, unlike other deep-water species, is large and has unusually strong concentric ridges and why the hinge plate is heavily calcified. Tropical molluscs tend to be more heavily calcified (Vermeij, 1978; Nicol, 1964; 1965, 1966 and 1967) and Moore, (1977) lists a number of heavily calcified endemic tropical nuculid species with strong concentric ridges. Conversely, reduced calcification is characteristic of deep-water species (Nicol, 1967) and is related to low temperatures and to high pressure (Grause, 1974). Thus, *N. pernambucensis* is unusual in this respect. Unfortunately no living shallow-water species similar to *N. pernambucensis* occurs in the tropical western Atlantic today (Moore, 1977), nor is there a similar species in the Holocene formations of Surinam even though a number of nuculids are present (Altena, 1968).

N. pernambucensis has the second-largest size of ovum of the species recorded here. The largest diameter recorded was 204 μm, sufficiently large to predict direct development rather than the more-typical lecithotrophic development with a free-swimming stage (Ockelmann, 1965).

Nuculoma perforata (new species)

Figs 17–19

TYPE LOCALITY: Atlantis II. Sta. 236, 36°27.0′S, 53°31.0′W, 518 m.

TYPE SPECIMEN: Holotype BM(NH) No. 1990008 from type locality; paratypes at present lodged at Woods Hole Oceanographic Institution (10 specimens in lot).

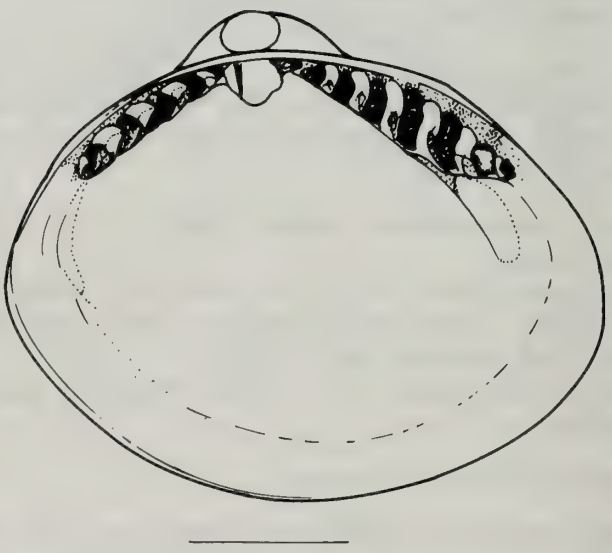

Fig. 13 *Nuculoidea pernambucensis*. Internal view of the left valve of a shell from Station 293. (Scale = 1.0 mm).

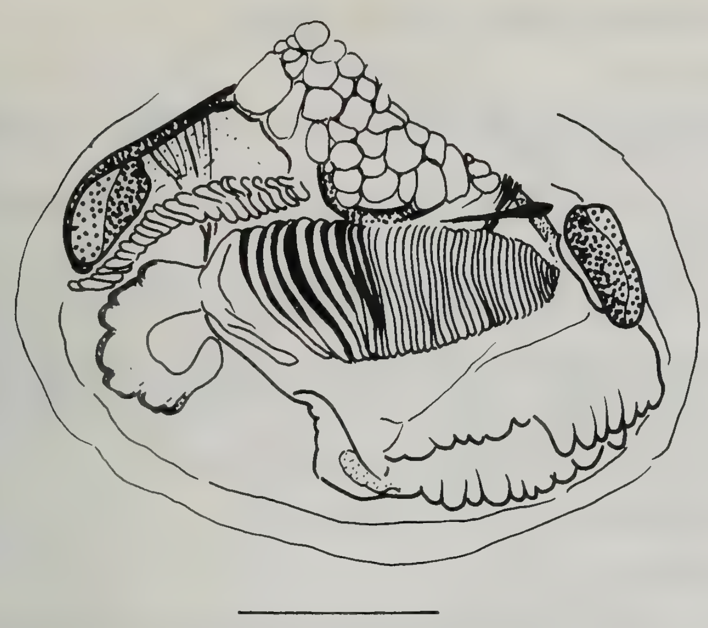

Fig. 14 *Nuculoidea pernambucensis*. Semidiagrammatic view from the right side of the body organs. (Scale = 1.0 mm). See figures 5 & 15 for identification of the parts.

DEPTH RANGE: 518–2323 metres.

MATERIAL

Cruise	Sta	Depth (m)	No	Lat	Long	Gear	Date
			ARGENTINE BASIN				
Atlantis II	236	518	15	36°27.0′S	53°31.0′W	ES	11.03.71
	237	1011	7	36°32.6′S	53°23.0′W	ES	11.03.71
	239	1679	37	36°49.0′S	53°15.4′W	ES	11.03.71
	240	2323	11	36°53.4′S	53°10.2′W	ES	12.03.71
	262	2480	1	36°15.1′S	52°1.79′W	ES	27.03.71
	264	2048	1	36°12.7′S	52°42.7′W	AD	28.03.71

SHELL DESCRIPTION

Shell small, elongate-ovate, equivalve, inequilateral; dentition usually visible through the dorsal part of the shell, smooth with fine concentric lines; umbo posterior to midline, opisthogyrate; when posterior margin orientated vertically, anterior dorsal margin is above horizontal; lunule usually bordered by tiny perforations, escutcheon, indistinct; resilifer oblique to narrow hinge plate, except in small specimens (<2 mm) extends ventral to anterior proximal teeth; hinge teeth chevron-shaped, the number varies with size, 3 posterior and 4 anterior teeth, in a specimen 1.6 mm in length and 4 posterior and 8 anterior teeth, in a specimen 4.7 mm in length.

SHELL MEASUREMENTS OF *Nuculoma perforata*

Dimension (mm)	No	Mean	SD	Max	Min
		ARGENTINE BASIN			
Length	20	2.95	1.7	9.04	1.42
Width		1.46	0.68	3.67	0.79
Height		2.24	1.27	6.54	1.07

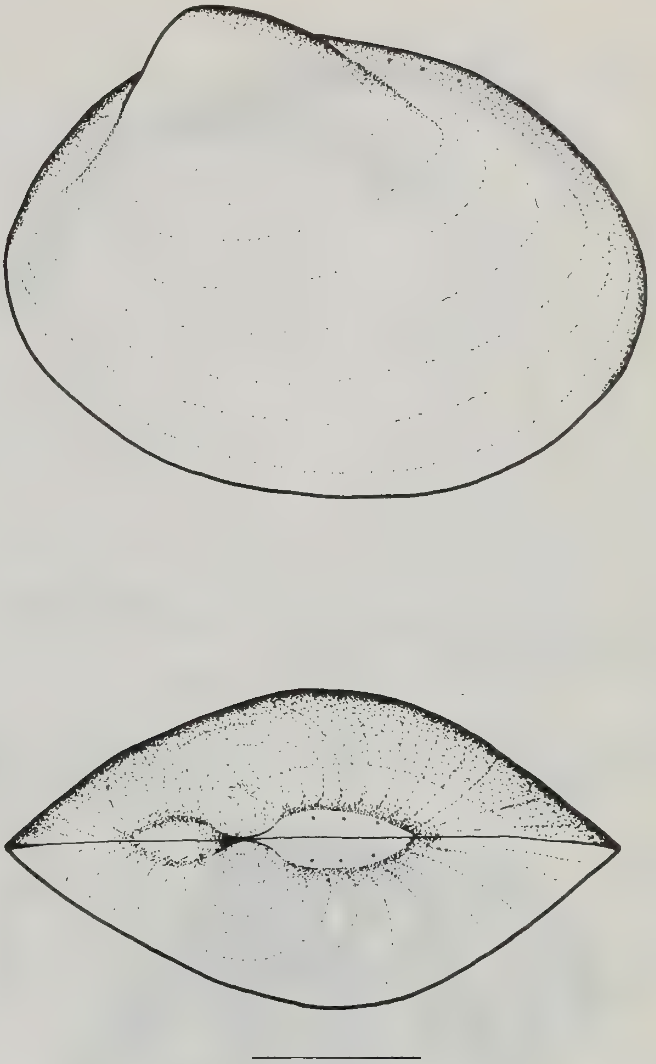

Fig. 15 *Nuculoma perforata*. Lateral and dorsal views of a shell from Station 239. (Scale = 1.0 mm).

INTERNAL MORPHOLOGY

The adductor muscles are oval in cross section the anterior being larger than the posterior (not obvious in Fig. 17 because of angle of view). The 'quick' and 'catch' portions are approximately equal. The gill axes lie parallel to the postero-dorsal margin of the shell. Gill plates number 18 in a specimen 3.7 mm in length. The palps are slightly smaller than those of *N. subovata* and do not extend to the posterior limit of the foot. There are also relatively fewer palp ridges (15 in a specimen 3.7 mm in length). The palp proboscides are typical but the 'byssal' gland is smaller than that of *D. atacellana*. This species has an exceptionally large stomach (Fig. 17).

DISTRIBUTION

Nuculoma perforata is restricted to the Argentine Basin. It appears to be closely related to the much-larger species *Nucula puelcha* d'Orbigny, 1842 from the adjacent continental shelf (Schenck, 1939). *Nucula puelcha* is similar to *Nuculoma tenuis* and should now be classified as a member of the genus *Nuculoma*. *N. puelcha* is present in WHOI collections from shallow-water stations adjacent to the Argentine Basin and we have considered the possibility that *N. perforata* may be young slow-growing specimens of *Nuculoma puelcha*, close to the limit of their bathymetric range. Although no mature specimens of *Nuculoma perforata* are present in the samples they differ in the configuration of the hindgut (Fig. 18) and furthermore they were more abundant at

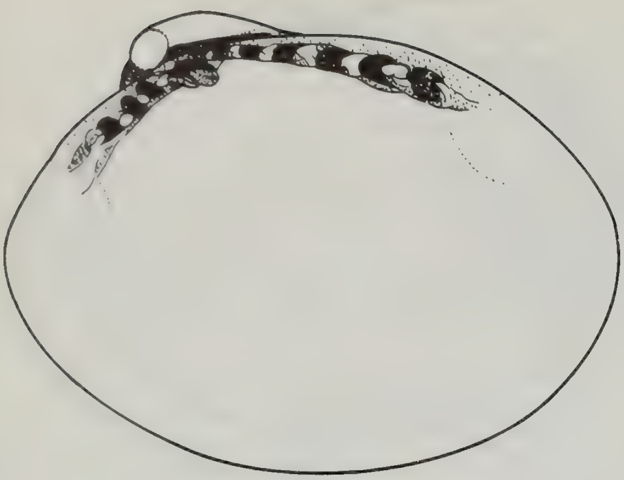

Fig. 16 *Nuculoma perforata*. Internal view of left valve of shell from Station 236. (Scale = 1.0 mm).

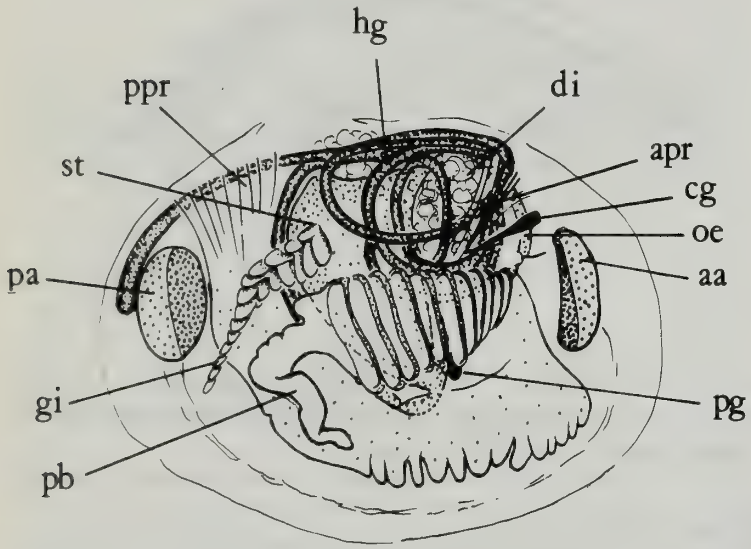

Fig. 17 *Nuculoma perforata*. Semidiagrammatic view of right side of the body to show arrangement of organs. (Scale = 1.0 mm; for key to abbreviations see p.63).

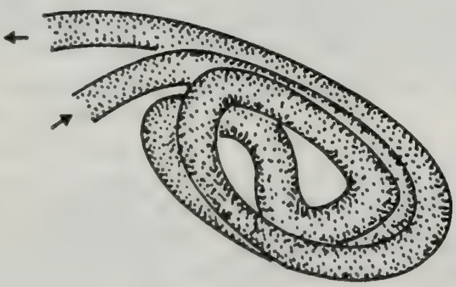

Fig. 18 *Nuculoma perforata*. The course of the hind gut as seen from the right side.

1670 m than at 507 m. We believe *N. perforata* to be a separate but closely related species to *N. puelcha*.

The species has some similarity with specimens dredged from relatively shallow water off the coast of Guyana (exact locality unknown) and named *Nucula surinamensis* by Altena, (1968).

Nuculoma granulosa (Verrill, 1884)

Figs 19–22

TYPE LOCALITY: Fish Hawk Sta. 892, Lat. 39°46′00″N, Long. 71°10′00″W, 891 m.

TYPE SPECIMEN: Holotype USNM No. 52561. (Examined JAA).

(Note: 5 specimens from Sarsia, Sta. S63, 46°17.5′N, 04°45.2′W, 1336 m lodged in BM(NH) No. 1990015).

Nucula granulosa Verrill, 1884, p. 280; Dall, 1889, p. 42; Verrill & Bush, 1898, p. 853, pl. 81, Fig. 2, pl. 88, Fig. 8; Johnson, 1934, p. 15.
Nucula cortica Grassle, 1977, p. 618; 1978, p. 42.

DEPTH RANGE: 811–2178 metres.

MATERIAL

Cruise	Sta	Depth (m)	No	Lat	Long	Gear	Date
			NORTH AMERICA BASIN				
Atlantis	F1	1500	33	39°47.0′N	70°45.0′W	AD	24.05.61
Atlantis II	73	1470	1143	39°46.5′N	70°43.3′W	ES	25.08.64
Chain	87	1102	844	39°48.7′N	70°40.8′W	ES	06.07.65
	103	2022	6	39°43.6′N	70°37.4′W	ES	04.05.66
	105	530	232	39°56.6′N	70°03.6′W	ES	05.05.66
Atlantis II	128	1254	5	39°46.5′N	70°45.2′W	ES	16.12.66
	131	2178	1	39°38.5′N	70°36.5′W	ES	18.12.66
Chain	207	811	161	39°51.0′N	70°56.4′W	ES	21.02.69
	209	1693	887	39°46.0′N	70°51.5′W	ES	22.02.69
	210	2064	6	39°43.2′N	70°49.5′W	ES	23.02.69
			WEST EUROPEAN BASIN				
Sarsia	S63	1336	31	46°17.5′N	04°45.2′W	ES	24.07.67
Challenger	ES20	1271	48	56°46.0′N	09°15.0′W	ES	23.09.73

Verrill, (1884) originally described the species as occurring in the North America Basin at U.S. Fisheries Commission stations 892, 1880, 1883 and 2072. This was later updated by Verrill & Bush, (1898) to include six stations between Lat. 39°43′45″N, Long. 70′7 W. and Lat. 36°47′N, Long. 73°9′30″W, in 2086–3340 m (station numbers were not given). Dall, (1889) describes the species as having a latitudinal range off the east coast of N. America from Georges Bank in the North to Cape Lookout in the South. This study extends its range to the Bay of Biscay and the Rockall Trough.

SHELL DESCRIPTION
The original description by Verrill, (1884) is not very detailed.

Shell very small, broad-ovate, equivalve, inequilateral, opaque surface smooth with fine concentric lines; umbo posterior to midline, opisthogyrate; when posterior margin orientated vertically, anterior dorsal margin is below horizontal; lunule bordered by angular ridge, escutcheon, indistinct; hinge teeth chevron-shaped, the number varying with size, 2 posterior and 3 anterior teeth in a specimen 0.94 mm in length, and 4 posterior and 6 anterior teeth in a specimen 1.98 mm in length; ligament large, perpendicular to relatively broad hinge plate, does not extend ventral to the anterior proximal teeth. Although the external shell morphology is somewhat variable, it must be regarded as a single species.

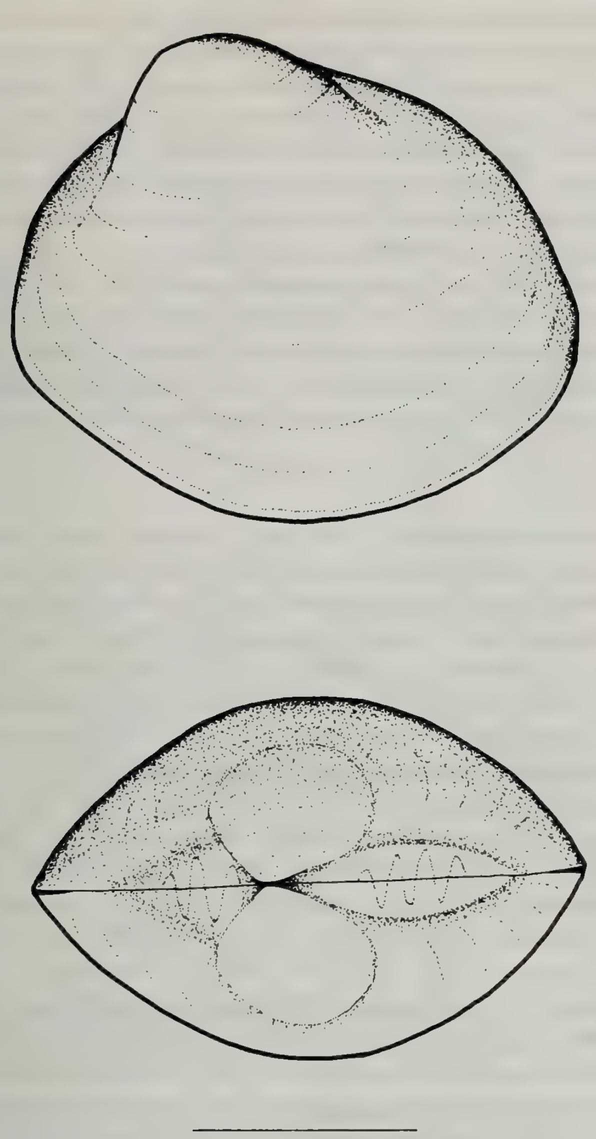

Fig. 19 *Nuculoma granulosa*. Lateral and dorsal views of a shell from Station 73. (Scale = 1.0 mm).

COMPARATIVE SHELL MEASUREMENTS OF *Nuculoma granulosa*

		NORTH AMERICA BASIN			
Length	22	2.05	0.28	2.45	1.39
Width		1.18	0.45	1.75	0.85
Height		1.81	0.27	2.26	1.22
		BAY OF BISCAY			
Length	10	1.76	0.16	1.93	1.42
Width		1.06	0.12	1.21	0.83
Height		1.54	0.14	1.69	1.21

INTERNAL MORPHOLOGY

The adductor muscles are oval and the anterior is larger than the posterior. The 'quick' and 'catch' portions are approximately equal. The gill axis lies parallel to posterior margin of the shell and the gill plates number 14 in a specimen ca. 2 mm in length. The palps do not extend to the posterior limit of the foot. The palp ridges number 16 in a specimen ca. 2 mm in length. The foot has a similar orientation and relative size to that of *Deminucula atacellana*, but the 'byssal' gland is narrower.

The hind gut configuration is also similar to that of *D. atacellana*. The maximum recorded diameter of the egg is

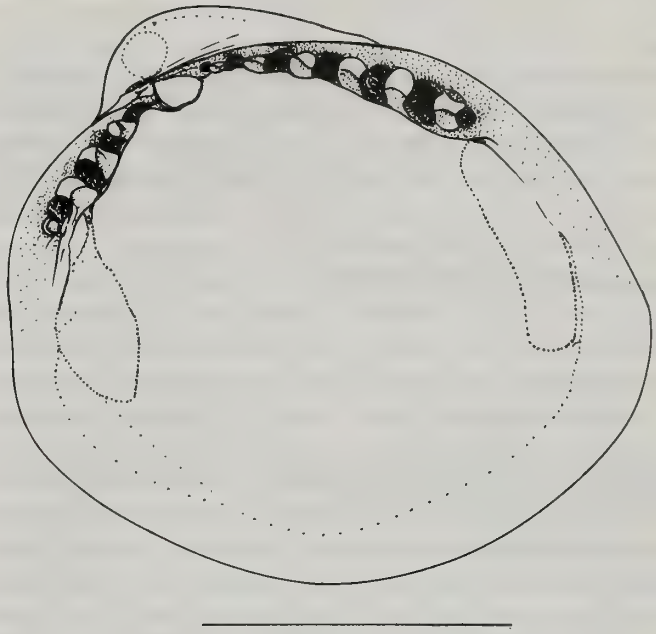

Fig. 20 *Nuculoma granulosa*. Internal view of left valve of shell from Station 563. (Scale = 1.0 mm).

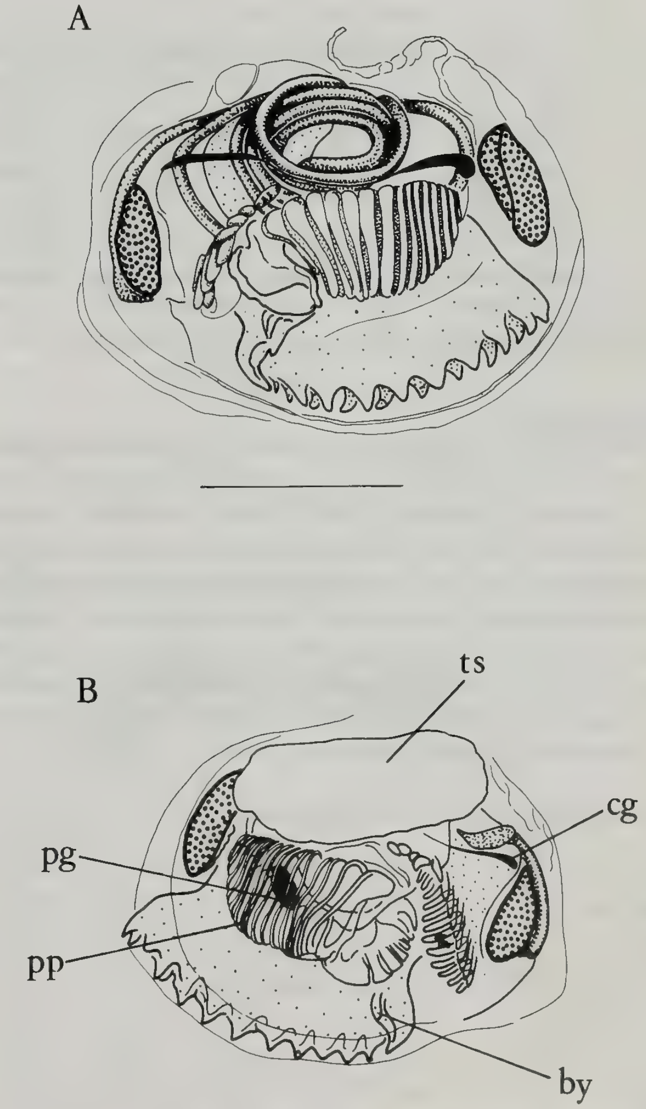

Fig. 21 *Nuculoma granulosa*. Semidiagrammatic views of A, right and B, left side of body of different specimens to show arrangement of body organs. (Scale = 1.0 mm; see Fig. 19 for identification of parts and for key to abbreviations see p.63).

120 μm (Scheltema, 1972) with approximately 220 eggs in a specimen 2.2 mm total length.

Distribution

It is an upper slope stenobathic species. It is closely related to *Nucula corticata* Möller, 1842 (Sowerby, 1871) a Greenland shallow-water species suggesting, as in the case of *Nuculoma similis* (see p.81 *et seq.*), a high latitude shallow-water derivation.

Nuculoma similis (new species)

Figs 23–25

Type locality: Chain Sta. 96, Lat. 39°55.2′N, Long. 70°39.5′W, 498 metres.

Type specimen: Holotype: BM(NH) No. 199005; Paratypes No. 1990006 (5 specimens in lot).

Depth range: 498–2064 metres.

Material

Cruise	Sta	Depth (m)	No	Lat	Long	Gear	Date
NORTH AMERICA BASIN							
Atlantis	E3	823	37	39°59.5′N	70°35.0′W	AD	25.05.61
Atlantis II	73	1470	126	39°46.5′N	70°43.3′W	ET	25.08.64
Chain	87	1102	270	39°48.7′N	70°40.8′W	ET	06.07.65
	88	478	34	39°54.1′N	70°37.0′W	ET	06.07.65
	96	498	86	39°55.2′N	70°39.5′W	ET	27.04.66
	103	2022	2	39°43.6′N	70°37.4′W	ET	04.05.66
Atlantis II	128	1254	27	39°46.5′N	70°45.2′W	ES	16.12.66
Chain	207	811	1348	39°46.5′N	70°56.4′W	ES	21.02.69
	209	1693	200	39°46.0′N	70°51.5′W	ES	22.02.69
	210	2064	1	39°43.2′N	70°49.5′W	ES	23.02.69

Shell description

Shell subtriangular, oblique, ventricose, equivalve, inequilateral; surface lustrous with fine concentric lines; umbos posterior to midline, opisthogyrate; when posterior margin orientated vertically, the antero-dorsal margin is below horizontal; indistinct lunule, chordate shaped escutcheon; hinge teeth chevron-shaped, the number varying with size, 1 posterior and 3 anterior teeth in a specimen 1.6 mm in length, and 3 posterior and 6 anterior teeth in a specimen 2.6 mm in length; ligament oblique to narrow hinge plate, extends slightly ventral to anterior proximal teeth.

Shell measurements of *Nuculoma similis*

Dimension (mm)	No	Mean	SD	Max	Min
NORTH AMERICA BASIN					
Length	71	1.97	0.420	3.03	1.19
Width		1.18	0.255	2.87	0.73
Height		1.62	0.351	1.61	1.01

Internal Morphology

The adductor muscles are approximately equal in size, more or less oval in shape. The anterior part of the gill axis lies parallel to the dorsal margin of the shell but posteriorly it curves to lie parallel to the posterior margin. The gill plates number 15 in a specimen ca. 3 mm in length. The palps are small with 16 palp ridges in a specimen of ca. 3 mm in length. In preserved specimens the foot is laterally compressed and the 'byssal' gland is extremely small. The stomach has an unusually small style sac. The hind gut configuration is not as complex as that of *Deminucula atacellana*.

N. similis has the largest ovum recorded for any species described in this paper (maximum diameter 244 μm). Scheltema, (1972) recorded a maximum egg size of 270 μm for *N. subovata* which was almost certainly a misidentification for *N. similis* (see p. 73). There can be little doubt that this species has direct development.

Distribution

This species is restricted to the North America Basin. In view of the intensity of past sampling in this Basin, it is curious that it has never been described previously, particularly as it is more abundant and has a greater vertical depth range than that of *Nuculoidea subovata* (p. 73). *Nuculoma similis* appears to be closely related to the Arctic shallow-water species *Nuculoma bellotii* (Fig. 26) (cf. 2 specimens from 181 m off Baffin Island BM(NH) No. 1990014).

The taxonomic status of *N. bellotii* has been disputed. Three Arctic species, *Nucula inflata* Hancock, 1846, *Nucula expansa* Reeve, 1855, and *Nucula bellotii* Adams, 1856, have been regarded as being conspecific with, or varieties of, *Nuculoma tenuis* (Gould, 1870; Whiteaves, 1901; Soot-Ryen, 1932; Filatova, 1948; Thorsen, 1951; Ockelmann, 1958; MacGinitie, 1959). Schenck, (1939) regarded the three Arctic species as synonymous and because the names *Nucula inflata* and *Nucula expansa* are homonyms the first available name is *Nucula bellotii*. Schenck accepted the subgenus *Ennucula* (Iredale) and named the species *Nucula (Ennucula) bellotii*. Schenck, (1939) also synonymized *N. bellotii* with the North

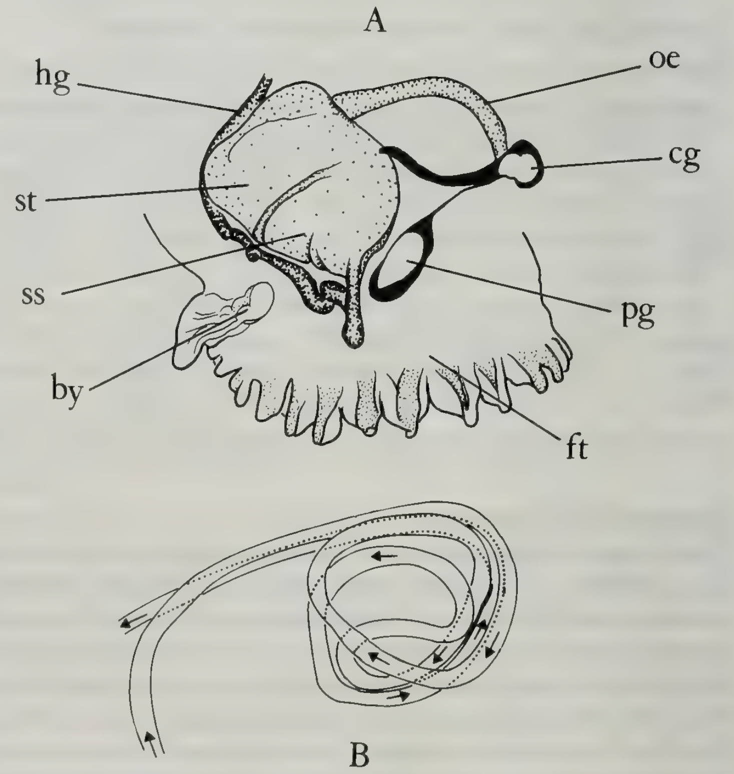

Fig. 22 *Nuculoma granulosa*. A. Detail of stomach and anterior part of nervous system and B. The course of the hind gut as seen from the right side. (For key to abbreviations see p.63).

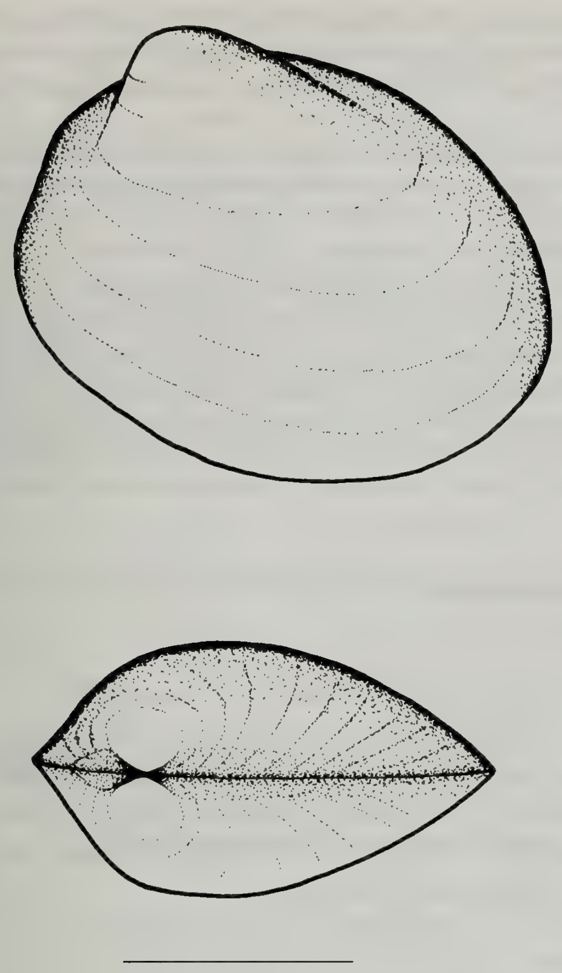

Fig. 23 *Nuculoma similis*. Lateral and dorsal views of shell from Station 207. (Scale = 1.0 mm).

Pacific species *N. quirca* Dall. Filatova, (1948) reports that an *inflata-expansa* complex (*N. bellotii*) as occurring in deep waters of the Barents and Bering Seas, while Lubinsky, (1972) also reported that specimens collected by Krause, (1885) from the Bering Straits and by MacGinity, (1959) from Point Barrow, and identified as *N. tenuis* Mont., *N. inflata* Hancock and *N. expansa* Reeve, were *N. bellotii*. Lubinsky's study indicates that *N. bellotii* occurs throughout the Canadian Arctic and she regards it as a circumpolar, panarctic species and separate from *N. tenuis*, however, she inferred that *N. bellotii* might be a subspecies of *N. tenuis*, although from comparisons of *N. tenuis* from Scottish waters, we doubt that. Both are species of the genus *Nuculoma*.

Bernard, (1979) collected specimens of *Nuculoma bellotii* from 132 stations throughout the Beaufort Sea. Abundant in depths <200 m it was also taken from depths down to 2560 m, showing that although *N. bellotii* is large (up to 20 mm in length) it is capable of deep-water existence. Recently Farrow *et al*., (1984) recorded *N. bellotii* from the Baffin Island fjords McBeth and Cambridge. These latter specimens were made available for comparative study (see Table below). Wagner, (1968) regarded fossil *Nuculoma bellotii*, collected by Bell, (1879) in the Hudson Bay area as part of the faunal assemblage of the Tyrrel Sea. Due to uplift much of this sea which reached its maximum extent between 5000 and 6000BC, disappeared with only remnants such as Hudson Bay and James Bay now remaining.

Nuculoma similis and *N. bellotii* share similar external shell features (eg. The characteristic 'pouting' of the anterior dorsal margin). As is usually the case with deep-sea species, specimens of *Nuculoma similis* are by far the smaller. The Table below lists the ratios of the height/length and width/length of *N. bellotii* taken from various localities (Lubinsky, 1972) compared with those of *Nuculoma similis*. Those of *Nuculoma similis* fall well within the range of *N. bellotii*. As in *Nuculoma similis*, the h/l and w/l ratios of *N. bellotii* are normally distributed (Lubinsky, 1972) and it is highly probable that *N. bellotii* and that inflated specimens (= *Nucula inflata* Hancock) and elongate, narrow ones (= *Nucula expansa* Reeve) are extreme variants of a unimodal population of a single species. If *Nuculoma similis* is a sibling species of *N. bellotii* it would help to explain why the former species only occurs in the North America Basin. Shallow-water specimens of *N. bellotii* from Baffin Bay and the Labrador Sea would presumably have been the origin of a sibling population adapted to deep water and early isolated in the North America Basin. That *N. bellotii* is not present on the New England shelf is probably due to it being a cold-water stenothermic species. The absence of *Nuculoma similis* from other Basins is probably related to the fact that it has direct development. Note that *N. bellotii* also has direct development, but from a much smaller egg (maximum diameter 163 µm). Stenothermy would also tend to isolate it to the deep sea and prevent it crossing boundary ridge systems. Both species are absent from the Norwegian Basin (Bouchet & Warén, 1979) which would suggest their centre of origin to be in the North Pacific.

SHELL MEASUREMENTS OF *Nuculoma bellotii* (from Lubinsky, 1972)

Species	Location	No	Length (mm)	h/l	w/l
Nuculoma bellotii	Foxe Basin	40	8–17	0.73–0.85	0.49–0.65
‘ ‘ ‘	Hudson Bay	80	6–12	0.70–0.90	0.49–0.67
‘ ‘ ‘	Ponds Inlet	10	7–14	0.77–0.82	0.47–0.67
‘ ‘ ‘	Wellington Ch & Frobisher Bay	14	10–16	0.78–0.86	0.49–0.68
‘ ‘ ‘	Labrador	16	10–16	0.79–0.90	0.54–0.64
Nuculoma similis	N. America Basin	71	1.19–3.03	0.79–0.89	0.54–0.65

Other Atlantic Arctic species to which *Nucula granulosa*

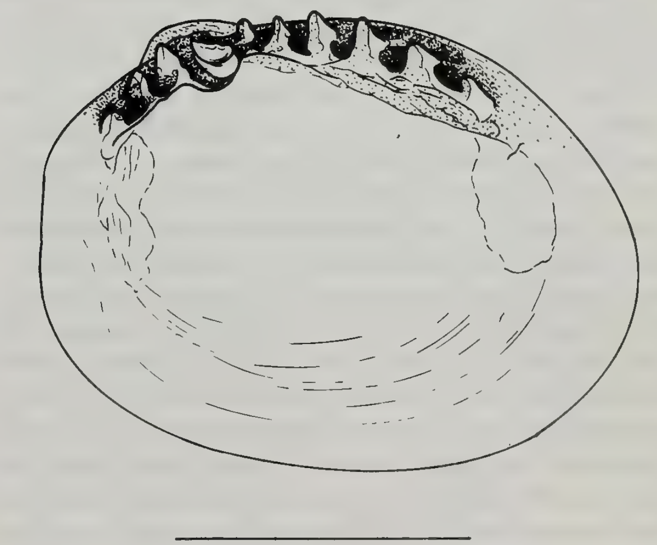

Fig. 24 *Nuculoma similis*. Internal view of left valve of shell from Station 96. (Scale = 1.0 mm).

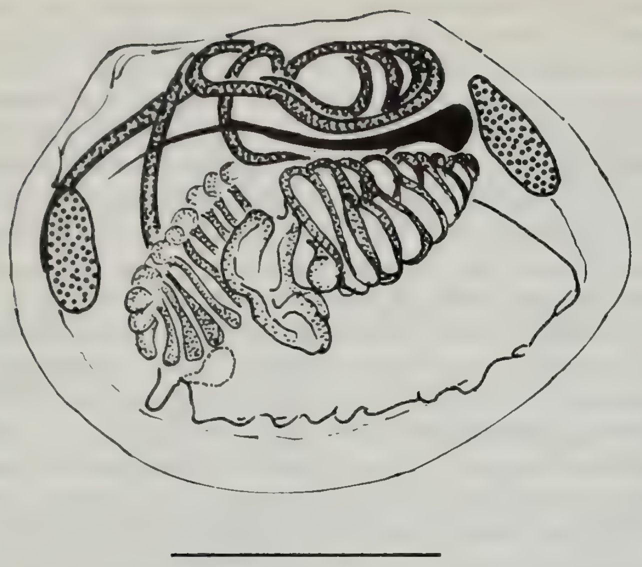

Fig. 25 *Nuculoma similis*. Semidiagrammatic view of right side of body to show arrangements of organs. (Scale = 1.0 mm; see Fig. 19 for identification of parts).

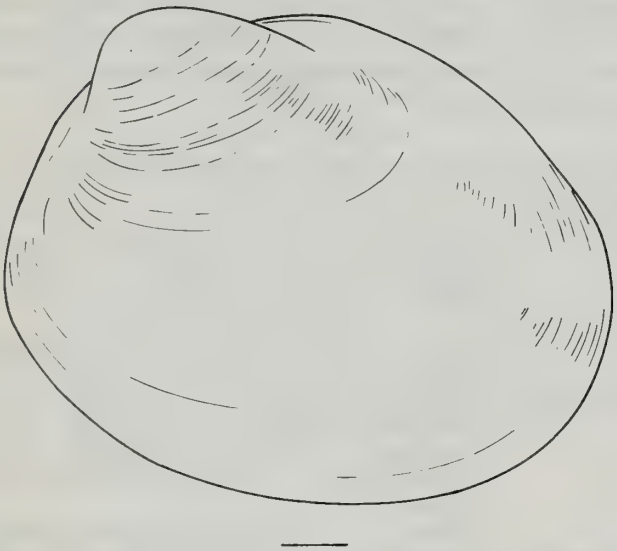

Fig. 26 *Nuculoma bellotii*. Lateral view of right valve of shell from Hudson Bay. (Scale = 1.0 mm).

and *N. similis* have possible similarity are *N. corticata* and *N. delphinodonta*. *N. delphinodonta* has a predominantly arctic shelf distribution, but off the Eastern Seaboard of the USA it extends south from Labrador to Maryland (Ockelmann, 1958; Abbott, 1974). Thus, its distribution is adjacent to that of *N. similis*. Furthermore, it has a large egg which has direct development, eggs being brooded in a secretion of the pallial gland attached to the posterior part of the shell. Although *N. similis* has a large egg, we have no evidence to indicate that brooding occurs. Although similar in shape and size, *N. delphinodonta* a short, stout species with a truncate posterior margin, can be distinguished by its coarse concentric growth lines, and a slight dorsal carination. Other differences include an average anterior to posterior hinge teeth ratio of 3:7 as compared with 3:6 for *N. similis*; the hinge teeth of *N. similis* are stouter and the hinge plates are broader particularly the anterior above which the antero-dorsal margin is more raised with greater curvature. Nevertheless, the two species appear to be closely related.

In comparison with *N. granulosa*, there is less similarity. *N. granulosa* is a much shorter species with fewer anterior hinge teeth and a shell outline that is significantly different from *N. delphinodonta*. *N. granulosa* has eggs of much smaller size, and almost certainly has a short, non-feeding, planktonic larva.

Comparison with *N. corticata* is much more difficult, simply because so little is known of this species. It was described as a Greenland species in Möller, (1842) and further described and illustrated by Sowerby, (1871) in Volume 18 of Reeve's *Conchologia Iconica*. There is little mention of it in the literature on the molluscan fauna of Greenland and Eastern Canada since then except that Soot-Ryan, (1966) records three specimens from the Michael Sars Expedition at 1100 m previously recorded as *N. tenuis* by Greig, (1920). Posteriorly the shell is rounded and not truncate as in *N. similis* and *N. granulosa*. Indeed, in outline *N. corticata* would appear to be similar to *N. tenuis expansa*.

Nuculoma elongata (new species)

Figs 27–28

TYPE LOCALITY: Knorr Sta. 297, Lat. 7°45.3′, Long. 54°24′W.

TYPE SPECIMENS: Holotype: BM(NH) No. 1990007 from type locality; paratypes at present lodged at Woods Hole Oceanographic Institution (2 specimens in lot).

DEPTH RANGE: 508–523 metres.

MATERIAL

Cruise	Sta	Depth (m)	No	Lat	Long	Gear	Date
			GUYANA BASIN				
Knorr	297	508–523	8	07°45.3′N	54°24.0′W	ES	28.02.72

SHELL DESCRIPTION

Shell very small, elongate-ovate, equivalve, inequilateral; surface smooth with fine concentric and radial striations, umbo posterior to midline, orthogyrate; when postero-dorsal margin orientated vertically antero-dorsal line is above the horizontal, posterior margin, dorsal to midline with faint concavity, lunule, bordered by tiny indistinct perforations, escutcheon, indistinct; ligament oblique to narrow hinge plate, not extending ventral to the anterior proximal teeth; 3 posterior and 4 anterior teeth in a specimen 2.1 mm in length.

SHELL MEASUREMENTS OF *Nuculoma elongata*

Dimension (mm)	No	Mean	SD	Max	Min
		GUYANA BASIN			
Length	5	1.75	0.24	2.01	1.47
Width		0.84	0.08	0.93	0.73
Height		1.30	0.15	1.47	1.11

INTERNAL MORPHOLOGY

The adductor muscles are oval in shape and approximately equal in size. The 'quick' and 'catch' portions are also approximately equal in size. The gill axis lies parallel to the posterior margin. There are eight gill plates and twelve palp ridges in a specimen ca. 2 mm in length. The foot is large and has a similar orientation to that of *Nuculoidea* and when retracted extends anterior to the anterior adductor muscle. The 'byssal' gland is large.

REMARKS

All specimens were collected from one station in the Guyana Basin from the upper slope in a depth of 508–523 m. A number of the larger specimens had mature gonads, indicating that they were not the young of a larger species. There is no species of similar shell shape and characteristics in adjacent waters.

Brevinucula verrilli (Dall, 1886)

Figs 29–32

TYPE LOCALITY: Albatross Sta. 2229, Lat. 37°38.40″, Long. 73°16.30″W, 2604 m.

TYPE SPECIMEN: Holotype: USNM No. 45752. Examined (JAA).

(Note: 4 specimens from Knorr Sta. 307, 12°34.4′N, 58°59.3′W, 3862 m, BM(NH) No. 1990016).

Nucula trigona Verrill 1885, p. 438; (*non* Bronn, 1849; *non* Seguenza 1877).
Nucula verrilli Dall, 1886, p. 248; 1889, p. 42; 1890, p. 257, pl. 14, Fig. 4; Bush 1893, p. 240, pl. 1, Figs 6, 7; Verrill & Bush, 1898, p. 853, pl. 95, Fig. 10; Clarke, 1962, p. 49; Pequegnat, 1972, p. 74.
Brevinucula verrillii Schenck, 1934, p. 41; James, 1972, p. 24–27, Figs 3, 4; map 1.
Brevinucula verrilli Knudsen, 1970, p. 19, Fig. 3, pl. 1, Figs 6, 7.
Nucula (Brevinucula) verrillii Haas, 1949, p. 7.
Nucula guineensis Thiele, 1931, p. 35; pl. 2, Figs 35, 35a; Clarke, 1962, p. 48, Knudsen, 1970.
Nucula (Brevinucula) guineensis Thiele, 1934, p. 786; Fig. 788.
Brevinucula guineensis Schenck, 1934, p. 4; pl. 5, Figs 22, 2c.
Nucula aequalis Barnard, 1964, p. 3365; Fig. 1c.

DEPTH RANGE: 1976–4749 metres.

The synonymy of this species has been much debated. Thiele, (1931) noted the similarity between *Nucula guineensis* and *B. verrilli*, however, while Schenck, (1934) regarded the two species as congeneric and probably conspecific, Clarke, (1962) recorded them as separate species. Later Knudsen, (1970) recorded them as conspecific and this view was upheld by James, (1972) who compared specimens from the Gulf of Mexico with the type (*N. trigona*, USNM No. 45752, and *Brevinucula guineensis*, Valdivia Sta. 56, ZMHU). Knudsen, (1970) also believes that *Nucula aequalis* (Barnard) is also synonymous with *Brevinucula verrilli*.

MATERIAL

Cruise	Sta	Depth (m)	No	Lat	Long	Gear	Date
			NORTH AMERICA BASIN				
Chain	77	3806	11	38°07.0′N	69°16.0′W	ES	30.06.65
	78	3828	6	38°08.0′N	69°18.7′W	ES	30.06.65
	84	4749	7	36°24.0′N	67°56.0′W	ES	04.07.65
	85	3834	21	37°59.2′N	69°26.2′W	ES	05.07.65
Atlantis II	119	2223	11	32°16.1′N	64°32.6′W	ES	19.08.66
	340	3356	12	38°14.4′N	70°20.3′W	ES	24.11.73
			WEST EUROPEAN BASIN				
Chain	321	2879	5	50°12.3′N	13°35.8′W	ES	29.08.72
	323	3356	3	50°08.3′N	13°53.7′W	ES	21.08.72
	329	4632	29	50°43.3′N	17°44.7′W	AD	23.08.72
			GUYANA BASIN				
Knorr	291	3868	10	10°06.6′N	55°15.4′W	ES	26.02.72
	299	2076	2	07°55.1′N	55°42.0′W	ES	29.02.72
	301	2500	18	08°12.4′N	55°50.2′W	ES	29.02.72
	303	2853	9	08°28.8′N	56°04.5′W	ES	01.02.72
	306	3429	27	09°31.1′N	56°20.6′W	ES	02.03.82
	307	3862	15	12°34.4′N	58°59.3′W	ES	03.03.72
			CANARIES BASIN				
Discovery	6704	2129	23	27°44.9′N	14°25.0′W	ES	17.03.72
	6707	2593	2	27°29.2′N	15°26.5′W	ES	17.03.68
	6709	2351	10	27°29.8′N	15°20.1′W	ES	18.03.68
	6710	2670	6	27°23.6′N	15°39.6′W	ES	19.03.68
	6711	2988	1	27°14.9′N	15°36.3′W	ES	19.03.68
			CAPE VERDE BASIN				
Atlantis II	138	1976	2	10°36.0′N	17°52.0′W	ES	04.12.67
	139	2187	3	10°33.0′N	17°53.0′W	ES	04.12.67
	141	2131	1	10°30.0′N	17°51.5′W	ES	05.02.67
	143	2095	4	10°35.0′N	17°44.0′W	ES	05.02.67
	144	2357	9	10°36.0′N	17°49.0′W	ES	05.02.67
	145	2185	10	10°36.0′N	17°49.0′W	ES	06.02.67
	146	2891	4	10°39.5′N	17°44.5′W	ES	06.02.67
	147	2934	51	10°38.0′N	17°52.0′W	ES	06.02.67
	148	3828	2	10°37.0′N	18°14.0′W	ES	07.02.67
	149	3861	7	10°30.0′N	18°18.0′W	ES	07.02.67
			MID ATLANTIC				
Atlantic II	155	3783	2	00°03.0′S	27°48.0′W	ES	13.02.67
			GUINEA BASIN				
Walda	DS25	2470	56	02°19.8′N	07°49.2′W	SD	00.00.71

SHELL DESCRIPTION

Except that he omits the fact that *B. verrilli* is without a well-defined resilifer, the original description by Verrill, (1885) is detailed and accurate.

Shell deeply triangular, robust, lustrous, equivalve, inequilateral; surface smooth, lustrous sometimes with fine irregular radiating striations; umbo approximately medial, orthogyrate, with faint ridge running from umbo to the postero-lateral angle; when postero-dorsal margin orientated vertically, antero-dorsal margin is below horizontal; lunule lanceolate, faint, escutcheon more distinct; resilifer not well-defined; ligament approximately triangular; hinge plate stout, hinge teeth chevron-shaped, the number varies with size, 4 posterior and 5 anterior teeth in a specimen 2.6 mm in length and 7 posterior and 9 anterior teeth in specimen 4.1 mm in length.

SHELL MEASUREMENTS OF *Brevinucula verrilli*

Dimension (mm)	No	Mean	SD	Max	Min
	NORTH AMERICA BASIN				
Length	7	2.31	1.05	3.94	1.06
Width		1.21	0.53	2.08	0.60
Height		2.25	1.11	4.06	0.99
	WEST EUROPEAN BASIN				
Length	29	2.35	0.75	3.95	1.00
Width		1.18	0.30	1.83	0.59
Height		2.33	0.77	4.04	0.93
	CANARIES BASIN				
Length	7	2.64	1.43	4.55	1.25
Width		1.37	0.68	2.41	0.73
Height		2.59	1.43	4.47	1.20
	CAPE VERDE BASIN				
Length	19	4.01	1.02	5.19	1.63
Width		2.02	0.53	2.87	0.97
Height		3.99	1.03	5.09	1.59

INTERNAL MORPHOLOGY

The posterior adductor muscles are more-or-less oval with the anterior muscle the more elongate and convex posteriorly. The 'quick' and 'catch' portions are approximately equal. The gill axis lies parallel to the postero-dorsal margin of the shell. The gill plates number 16 in a specimen 3.9 mm in length. The palps are moderately large and, in the same specimen, the palp ridges number 27. The 'byssal' gland is large. The stomach is relatively small and the hind gut is extensive (Fig. 31). Note the course of the gut is complex even to the extent that a few loops are to the left of the stomach. The species has large characteristic loosely arranged gonads. The maximum recorded egg diameter is 125 μm and development is likely to be lecithrotrophic. There are 260 eggs in a specimen 4.3 mm total length (Scheltema, 1972).

The species was originally described as having a triangular 'chondrophore' and, as Vokes, (1949) points out, although this is unique among Recent nuculids, it occurs in the Palaeozoic species *Nuculoidea opima* Hall and *Nuculopsis girtyi* Schenck. More-recent studies show that although the hinge plate is broad *B. verrilli* is without a chondrophore but has a well-developed resilifer (Allen & Hannah, 1986). This may also be the case in the Palaeozoic species. According to Moore, (1969) *B. verrilli* is not present in the fossil record prior to the Miocene.

DISTRIBUTION

B. verrilli is restricted to the deep sea and no comparable shallow-water counterpart exists.

Verrill, (1885) collected the species from the North America Basin at U.S. Fisheries Commission Stations 2194, 2228 and 2229 at depths ranging from 2086–4077 m. Dall, (1890) reported specimens from Station 2754, east of Tobago and Station 2760, north from Ceara, Brazil in 1610 and 1865 metres respectively and summarized the then known geo-

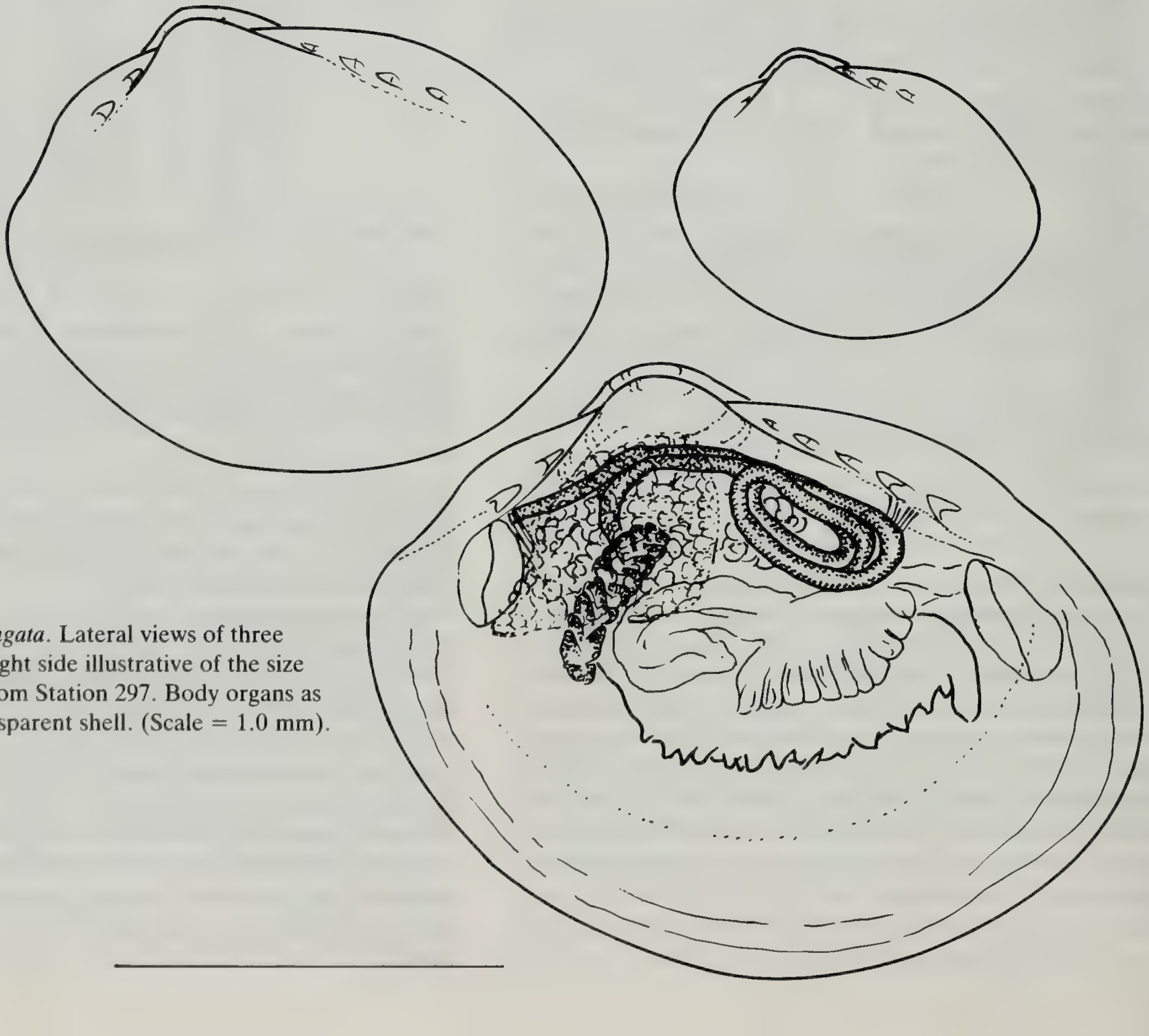

Fig. 27 *Nuculoma elongata*. Lateral views of three specimens from the right side illustrative of the size range of specimens from Station 297. Body organs as seen through the transparent shell. (Scale = 1.0 mm).

graphical distribution as from latitude 39°44′, south to Yucatan at depths from 538 to 3340 metres (Dall, 1927). Thiele, (1931) described *N. guineensis* from the Guinea Basin ('Valdivia' Stations 56, 63 and 71) and Knudsen, (1970) set the latitudinal limits from 40°N to 12°S in the western Atlantic and from 4°N to 6°S in the eastern Atlantic. Pequegnat, (1972) reported the species from the gulf of Mexico and this was confirmed by James, (1972) who collected from 12 Stations in depths from 914 to 3475 metres.

The report (Knudsen, 1970) that the species occurs at 12°S in the western Atlantic is not confirmed. Specimens taken from this latitude differ from *Brevinucula verrilli*. Little material was taken from the Brazil Basin and the absence of *B. verrilli* may be related to insufficient sampling.

B. verrilli is predominantly a North Atlantic species. Its distribution in the temperate eastern Atlantic is now extended to 50°N. Despite intensive sampling it is not recorded from the Rockall Trough and Bay of Biscay and the reason for this is not immediately apparent. It has a vertical range that extends into depths shallower than both these regions. No comparable species occurs in the angola and the Argentine Basins, however, Barnard, (1962), described *Nucula aequalis* from off Cape Point, South Africa and this may be synonymous with *B. verrilli* (Knudsen, 1970). If this is correct it could be that this is a case of a species with bipolar distribution Ekman, (1953). This phenomenon is unusual among deep sea bivalves and would be the first reported case of an abyssal bivalve to have such a distribution.

B. verrilli occurs at greater depths than any other member of the Nuculidae and its distribution extends on to the abyssal plain.

Brevinucula subtriangularis (new species)

Figs 33–34

TYPE LOCALITY: Atlantis II Sta. 167, Lat. 7°58′S Long. 34°17′W.

TYPE SPECIMEN: Holotype: BM(NH) No. 1990009; paratypes at present lodged at Woods Hole Oceanographic Institution (5 specimens in lot).

DEPTH RANGE: 943–1007 metres.

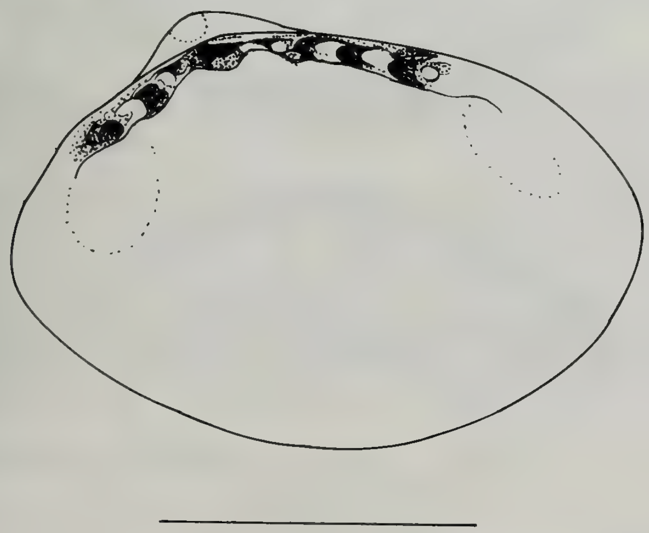

Fig. 28 *Nuculoma elongata*. Internal view of left valve of shell form Station 297. (Scale = 1.0 mm).

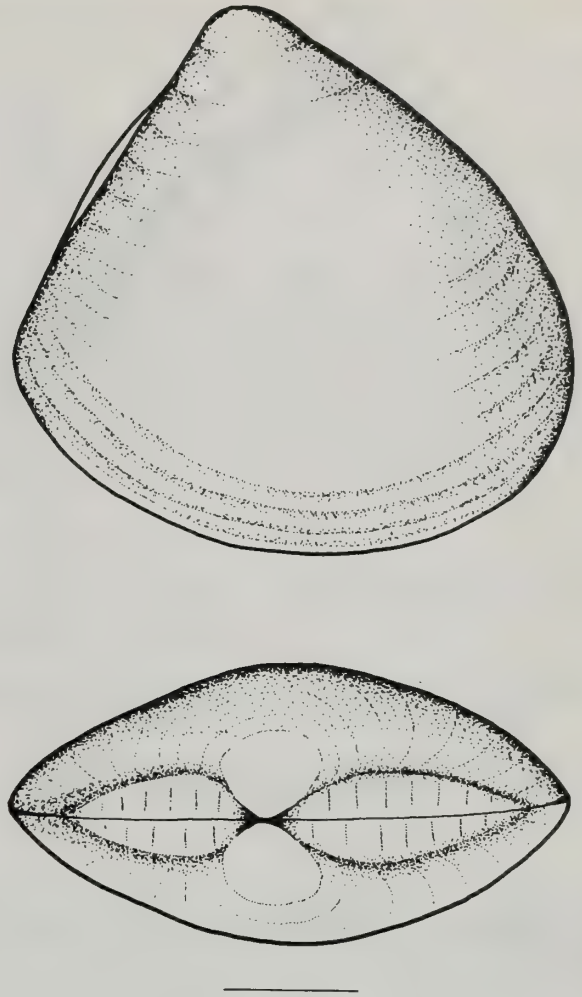

Fig. 29 *Brevinucula verrilli*. Lateral and dorsal view of a shell from Station 85. (Scale = 1.0 mm).

MATERIAL

Cruise	Sta	Depth (m)	No	Lat	Long	Gear	Date
			BRAZIL BASIN				
Atlantis II	167	943–1007	31	07°58.0′S	34°17.0′W	ES	20.02.67

SHELL DESCRIPTION

Shell small, robust, lustrous, very smooth, equivalve, inequilateral; umbo posterior to midline, opisothygrate; when posterior margin orientated vertically, antero-dorsal margin is horizontal; lunule indistinct, escutcheon marked by faint ridge from umbo to the postero-ventral angle; resilifer large; ligament approximately triangular; hinge plate stout, hinge teeth chevron-shaped, 5 posterior and 9 anterior teeth in a specimen 4.9 mm in length.

SHELL MEASUREMENTS OF *Brevinucula subtriangularis*

Dimension (mm)	No	Mean	SD	Max	Min
		BRAZIL BASIN			
Length	2	4.95	0.06	5.00	4.91
Width		2.98	0.44	3.29	2.67
Height		4.58	0.15	4.69	4.48

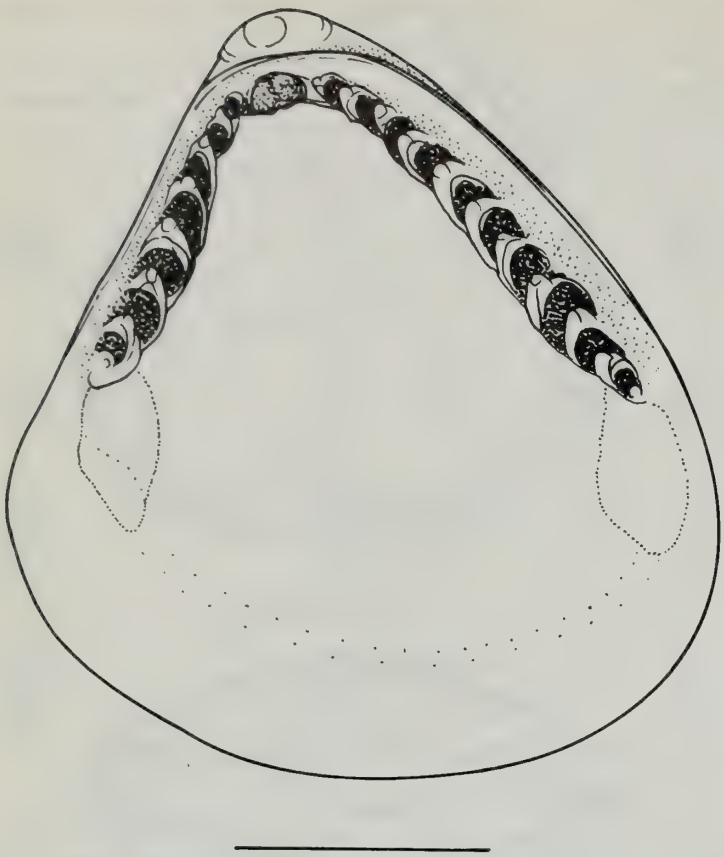

Fig. 30 *Brevinucula verrilli*. Internal view of left valve of shell from Station 85.

INTERNAL MORPHOLOGY

The adductor muscles are more or less oval. The anterior muscle is larger than the posterior and both have a shape similar to those of *B. verrilli*. The 'quick' and 'catch' portions are approximately equal in size. The gill axis is parallel to the posterior margin of the shell with 15 gill plates in a specimen

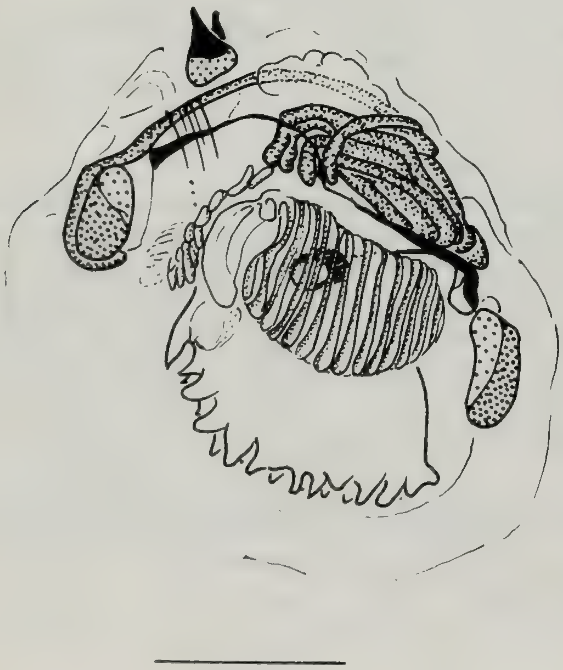

Fig. 31 *Brevinucula verrilli*. Semidiagrammatic view of right side of body to show arrangement of organs. (Scale = 1.0 mm; see Fig. 19 for identification of parts).

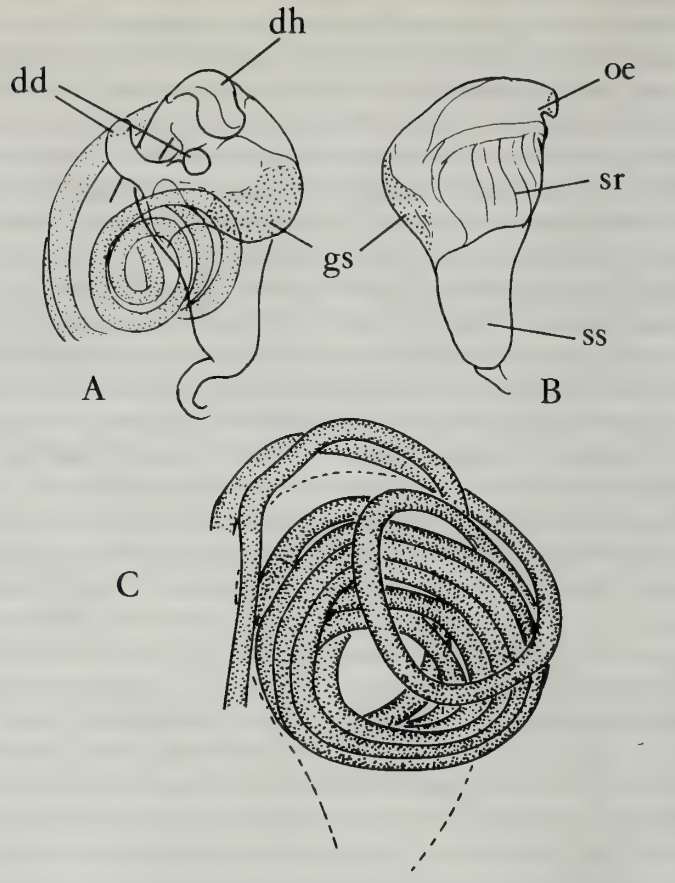

Fig. 32 *Brevinucula verrilli*. A. Lateral view of left side of stomach, and coils of hind gut on the left side of stomach; B. Lateral view of the right side of stomach to show posterior sorting area; C. The coils of the hind gut to the right side of the stomach, the stomach outlined by dashed lines. (For key to abbreviations see p.63).

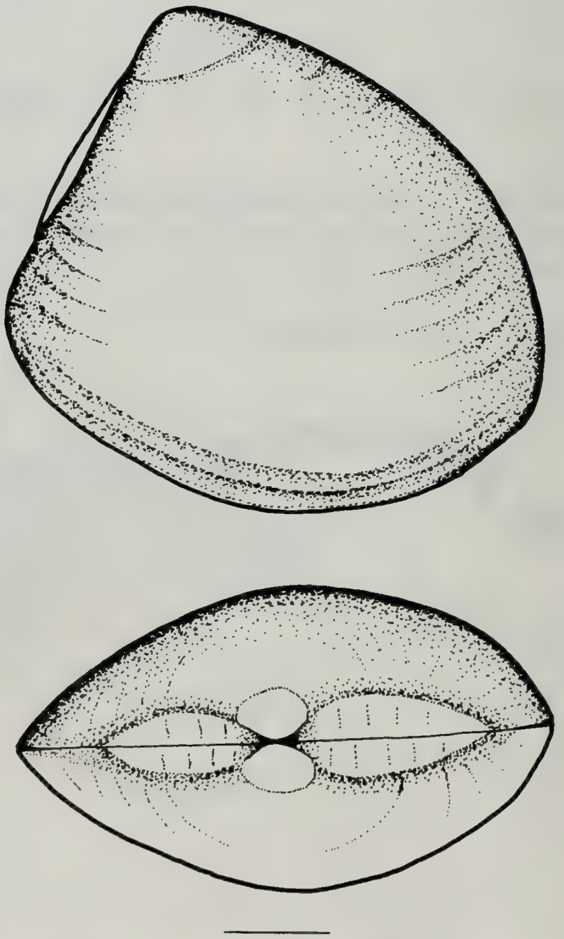

Fig. 33 *Brevinucula subtriangularis*. Lateral and dorsal view of a shell from Station 167. (Scale = 1.0 mm).

5 mm in length. The palps are moderately large and there are 28 palp ridges in the same specimen. The foot is similar in proportion and orientation to that of *B. verrilli*. The 'byssal' gland is large. The stomach is relatively small and the hind gut is extensive. The gonads are large and loosely arranged.

Although this species differs in shape from *B. verrilli* eg. The shells are slightly longer than high, they have features in common. They have a very large resilifer, and have a non-crenulate inner ventral shell margin. Both species have rounded anterior and posterior shell margins. *B. subtriangularis* is slightly heteromyarian, and the shape of the anterior adductor muscle is similar to that of *B. verrilli*. Both species have a comparatively small stomach, and large, loosely arranged gonads.

Distributions

Brevinucula subtriangularis was collected from one Station at mid-slope depth from the Brazil Basin. No comparable species are present in the Holocene formations of Guyana (Altena, 1968), even though species of *Brevinucula* appear to have been common in Jurassic and Triassic shallow seas.

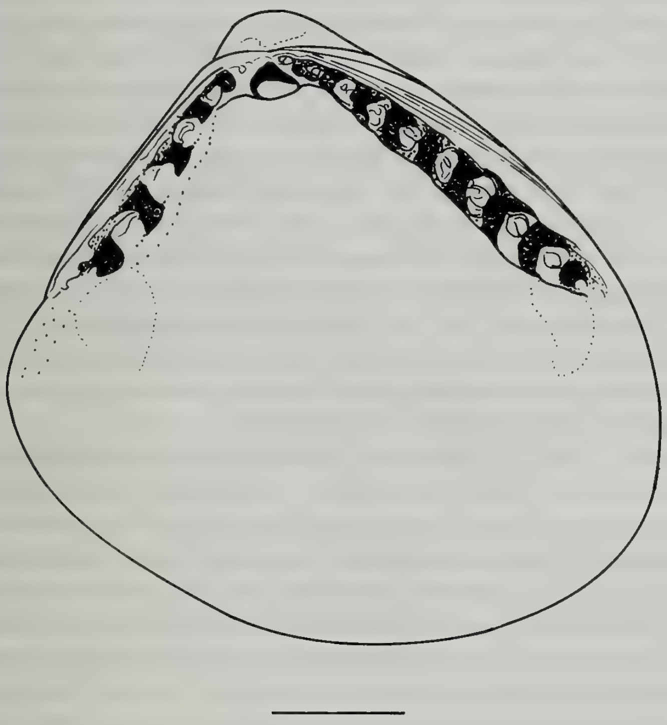

Fig. 34 *Brevinucula subtriangularis*. Internal view of left valve of shell from Station 167. (Scale = 1.0 mm).

OTHER ATLANTIC DEEP-SEA NUCULIDS

Here we list species not discussed so far in the text that have been described as having a deep-sea distribution. This latter we construe as having a population 'peak' below 500 metres, clearly below the shelf-slope break. We have excluded species from the Norwegian Basin in that its abyssal bivalve fauna is almost without exception self-contained (Bouchet & Warén, 1979).

Nucula crenulata Adams, 1856

Type locality: Guadaloupe.

Type specimen: Probable syntype, BM(NH) 1991012 (examined PR).

Nucula crenulata Adams, 1856; Dall, 1886, p. 247, pl. 7, Fig. 2 (in part); 1889b, p. 42, pl. 8, Fig. 2.
Nucula crenulata var obliterata Dall, 1881, p. 123; Clarke, 1962, p. 48.
Nucula culebrensis obliterata Johnson, 1934, p. 16.
Nucula obliterata James 1972, p. 39–40, Figs 19, 20, Map 2; (*non Nucula obliterata* Knudsen, 1970).

Dall, (1881, 1886, 1890) reported this species from the Florida Straits, the south east of the Gulf of Mexico, the southeastern Caribbean, and off Cape Hatteras from depths of 168 to 1472 metres James, (1972) also recorded the species from the Gulf of Mexico from depths of 969 to 1280 metres.

N. crenulata resembles the Tertiary species *Nucula striatissima* Seguenza.

Nucula culebrensis Smith, 1885

Type locality: 'Challenger' Sta. 14, Lat. 18°38′30″N, Long. 65°05′30″W, 714 m.

Type specimen: Holotype not designated; syntypes (5 valves, BM(NH) 1887.2.9.2912–3) (examined PR).

Nucula culebrensis Smith, 1885, p. 228, pl.18, fig. 11, 11a; James, 1972, p. 36–38, Figs 15, 16, Map 2.

Remarks

The original description by Smith, (1885) is detailed. The species is similar in shape to *Deminucula cancellata* but differs in having tubercles that surround the lunule. The species originally taken off the West Indies is also recorded in the Gulf of Mexico 417–1518 metres (James, 1972), however, these latter shells were badly eroded and were thought to have been vertically displaced.

Deminucula fernandinae (Dall, 1927)

Type locality: 'Albatross' Sta. 2668, Lat. 30°58′N, Long. 79°38′W, 678 m.

Type specimen: Holotype not designated, but syntypes (two pairs conjoined valves and one valve) exist: USNM No. 108198 (examined JAA).

Nucula fernandinae Dall, 1927, p. 8; Johnson, 1934, p. 16.

Dall, (1927) gives only a brief description but compares *D. fernandinae* with *N. culebrensis* and *N. crenulata var obliterata*.

This species was described from two whole specimens and one larger valve (Dall, 1927). A single left valve of this species is also recorded by James, (1972) from the Gulf of Mexico in 2528 metres but is probably vertically displaced. This species is similar to *D. atacellana* and like this species has a prominent concentric sculpture and is without a well-defined resilifer.

Nucula zophos Clarke, 1960

Type locality: 'Alpha' Sta. 6, Lat. 84°28′N, Long. 148°28′W, 1691 m.

Type specimen: Holotype: Mus. Comp. Zool. Harv. No. 222067 (examined JAA).

Nucula zophos Clarke, 1960, p. 5; pl. 1, Figs 15–18, 1963,

p. 99; Paul & Manzies 1973, p. 127; Bernard, 1979, p. 11, Fig. 2; Knudsen, 1985, p. 98.

The original description by Clarke, (1960) is detailed. The species was found by Clarke, (1960) about 800 miles north of Port Barrow, Alaska, in depth ranges from 1464–1660 metres. Bernard, (1979) has also collected the species from 2377 m in the Beaufort Sea. Bernard, (1979) states that the species is widely distributed in the archibenthal of the Laurentian Basin. Knudsen, (1985) records the species off northeast Greenland and from 530–2237 metres—a much greater range than found by Bernard, (1979). The species appears to be restricted to the Polar and Laurentian Basins and has not been reported south of the Iceland-Faeroe ridge nor, surprisingly in the Norwegian abyssal basin (Bouchet & Warén, 1979). It bears a close resemblance to *N. callicredemna*.

Pronucula benguelana Clarke, 1961

TYPE LOCALITY: R/V Vema Sta. 14, Lat. 30°14.9′S, Long. 13°03′E, 3116 m.

TYPE SPECIMEN: Holotype: Mus. Comp. Zool. Harv. No. 224964 (examined JAA).

Pronuncula benguelana Clarke, 1961, p. 368–369, pl. 3, Figs 9, 11.
Nucula (Pronucula) benguelana Barnard, 1962, p. 446; Fig. 11a.

The original description by Clarke, (1961) is detailed, but although Clarke, (1961) described this species as having a non-crenulate ventral margin, *Pronucula benguelana* has radial sculpturing which is typical of species with marginal crenulations and we confirm Barnard, (1962) who describes the species as having a crenulate margin. Note: Barnard regards *Pronucula* as a subgenus of *Nucula*.

This species, which is not present in any of the Atlantic abyssal material reported on in this study, appears to be restricted to the Cape Basin (Clarke, 1961). It has been described by Barnard, (1962) as occurring west of Cape Point, South Africa and, according to Clarke, (1961) it is a member of a deep-sea species complex present in the southern Indian and Pacific Oceans.

Finally brief mention should be made of *Nuculoma corbuloides* (Seguenza, 1877) and *Nucula striatissima* (Seguenza, 1877). Both species were described from Tertiary fossils. Thereafter Recent specimens from the Mediterranean and the Eastern Atlantic are listed in Jeffreys, 1879, Locard, 1898, and Massey, 1930. These specimens are relatively few in number and taken from slope depths. Despite extensive sampling by French workers in the Bay of Biscay these species have not been recorded in recent years.

ORIGIN, ANTIQUITY & DIVERSITY OF THE DEEP-SEA NUCULIDS

The abyss has been regarded as a sanctuary for an archaic relict fauna (Ekman, 1953; Dahl, 1954; Zenkevitch & Birstein, 1956, 1960; Birstein, 1959, 1969; Zenkevitch, 1969) and there are many claims that 'living fossil' representatives of groups occur eg. Radiolaria (Haecker, 1908), Hexactinellida (Ijima, 1927), Crinoidea (Clark, 1915), Asteroidae (Zenkevitch & Birstein, 1956), Holothurioidea (Theel, 1882), Harpacticoida (Zenkevitch & Birstein, 1956), Mysidacea (Tattersall, 1921), Isopoda (Wolff, 1956a), Tanaidacea (Wolff, 1956b), Decapoda (Doflein, 1904; Balss, 1925, 1955), Pisces (Andraishev, 1953) and Mollusca (Locard, 1898; Bonnevie, 1912; Zenkevitch & Birstein, 1960; Parker, 1962; Filatova, 1959; Filatova *et al.*, 1968). The majority of deep sea bivalves belong to groups whose geological record dates back to the Ordovician (Allen, 1978).

The dominant bivalve group of the deep sea, the Protobranchia, is present in the earliest assemblages of the fossil record and protobranch genera such as *Tindaria, Malletia, Neilonella, Neilo, Nuculana, Yoldia, Yoldiella* and *Nucula* are regarded by Zenkevitch & Birstein, (1960) as ancient elements of the deep-sea fauna. In contrast relatively few protobranch species occur in shelf seas and these are almost entirely restricted to the families Nuculidae and Nuculanidae (Allen, 1978).

Of the divisions of the Nuculidae as defined by Schenck, (1939) (p. 64) two occur in the deep Atlantic namely those with crenulate shell margins and those with smooth shell margins. Species with divaricate shell sculpture do not occur (nor do they occur in shallow waters of the Atlantic).

Species with smooth margins are found throughout geologic time. One of the earliest from the Pennsylvanian of Iowa, *Nuculopsis ventricosa* (Hall) has a shell morphology that differs little from Recent species (Schenck, 1939). Species of *Nuculoidea* date from the Silurian and Devonian (McAlester, 1962; Soot-Ryen, 1964). *Nuculoma* dates from the Jurassic (Cossmann & Thiery, 1907). In contrast crenulate species have a far less protracted geologic history and extend no further back than the Cretaceous (a possible exception is the Mississippean Carboniferous species *Nucula schumardiana* (Cox, 1940; Vokes, 1949).

Vokes, (1949) also reported the Palaeozoic species '*Nuculoidea opima* Hall' as having microscopic crenulations. Because this did not fit into the Schenck, (1939) classification Vokes, (1949) suggested that such species should be placed in a separate group from the crenulate and non-crenulate forms. This includes the species of *Brevinucula*. Moore, (1969) states that *Brevinucula* does not appear in the geological record prior to the Miocene.

Thus, the present study supports the concept of antiquity. Species with non-crenulate inner ventral shell margins are descended from a more-archaic group than species with a crenulate inner ventral margin and the former, which have representatives in the Ordovician, are far the more abundant in the deep sea. In contrast, the crenulate species which did not appear in the fossil record until the Cretaceous are more abundant in shallow water. Of 12 shallow-water nuculids of the North Atlantic, 4 have non-crenulate shell margins, whereas of 8 deep-sea Atlantic species (not including *Brevinucula*) 6 have non-crenulate margins. As Knudsen, (1970) suggests, there probably has been a descent of shallow-water species into the abyssal zone throughout geological history. Therefore it would be expected that along with species of deep-water origin there exist deep-water species closely related to shallow-water species. Zenkevitch & Birstein, (1960) suggest that it is possible to distinguish between ancient and secondary deep-water species by their patterns of distribution. In the case of the secondary species, their diversity decreases with increasing depth whereas the ancient groups tend to show increasing diversity with increasing depth which diminishes only when encroaching lower abyssal depths or the perturbed trenches and vent systems. The distribution pattern of deep-sea 'non-crenulate' nuculids would suggest that they are an ancient rather than a secondary deep-water group.

It has been assumed that one of the more important factors restricting downward migration is temperature and that polar coastal regions yield species of the necessary eurybathic capacity to invade the deep sea (Bruun, 1956; Kussakin, 1973). The close affinity between the Arctic shallow-water species, *N. bellotii* and *Nuculoma similis* and the Greenland species *N. corticata* with *N. granulosa* would appear to support this conclusion.

Kussakin, (1973) noted that primitive isopods are principally confined to tropical waters, whereas isopods of cold and temperate regions and especially the deep-sea are considered phylogenetically recent. He speculated that tropical faunas gave rise to temperate faunas which then gave rise to cold-water faunas and that from the cold-water faunas of the Antarctic shelf came the initial and main source of deep-sea faunas. The adaptation of the shelf fauna to deep-sea conditions was thought to have been promoted by climatic cooling and subsequent glaciation which occurred in the Miocene and approximately a million years earlier than in the northern hemisphere, and therefore Antarctica became the sole zone supplying cold oxygen bearing water into the abyssal zone. The thickening ice was thought to cause the gradual isostatic dipping of the continent and shelf by as much as 900 m and so the Antarctic shelf-fauna was slowly forced deeper. The movement of cold Antarctic water into the abyss and then northwards would have then facilitated subsequent distribution. In contrast to Kussakin, (1973), Hessler *et al.*, (1979) also on the basis of biogeographical studies of deep-sea isopods, argue that the presence of species closely related to deep-sea species in shallow high latitudes is the result of subsequent emergence and that many deep-sea species evolved *in situ*.

Curiously, although evidence suggests that a few deep-sea nuculids had their origin in the Arctic region, there is no indication that a similar process occurred in the Antarctic. There is a dearth of nuculids in the deep Antarctic (Dell, 1972) and to date only *N. notobenthalis* Thiele, has been described and this does not appear to be similar to any other deep-sea Atlantic species. It is perfectly feasible that 'non-crenulate' nuculids, which are more diverse in the deep sea, may have given rise to shallow water species such as *Nuculoma tenuis* and *N. bellotii*. Some abyssal genera are cosmopolitan and thus they are potentially available for emergence into any suitable shallow-water environment (Hessler *et al.*, 1979). This would explain the ubiquity of *N. tenuis*.

There are two strict shallow-water nuculids in the Arctic (Clarke, 1960; Bernard, 1979), 7 or 8 species occur in the temperate zone (5 on the east coast of the North Atlantic (Allen, 1954), and 3 or 4 on the west coast (Mighels & Adams, 1842; Hampson, 1971; Abbott, 1974). Six species occur in the western tropical region between the Caribbean and Surinam (Dautzenberg, 1900; Weisbord, 1964; Altena, 1968; Moore, 1977). There does not appear to be any certain information relating to the number of species present in the eastern tropical Atlantic, but there is likely to be a further assemblage of species. On this basis nuculid diversity would appear to increase slightly towards the tropics. Prior to the radiation of the other major shallow water bivalve deposit-feeding group the Tellinacea, in the middle Cretaceous nuculid diversity in the tropics was probably far greater and, since the 'crenulate' nuculid species did not evolve until the Cretaceous, the assemblages would presumably have been mainly composed of 'non-crenulate' forms. Tellinaceans are not present in the abyss and only two species are present at lower slope depths (Allen & Sanders, 1966), but massive radiation of tellinaceans may have resulted in the extinction of the shallow water tropical nuculid predecessors and may eventually lead to the loss of others in higher latitudes and the deep-sea. This totally ignores physiological aspects which presently constrain the colonization of the deep-sea by tellinaceans and favour the nuculacean presence there (Allen, 1978).

Sanders & Hessler, (1969) found that in general, diversity in abyssal basins was of a similar order of magnitude to that found in some shallow tropical seas and well exceeds that in cold temperate shelf seas. Unlike the nuculanids the vertical diversity of the nuculids does not conform to this generalization. Although, there is an increase in the diversity of 'non-crenulate' species with depth, overall nuculid diversity decreases. For example, on the temperate North East Atlantic shelf (<200 m) there are 5 species (Allen, 1954), whereas in the West European Basin (>1500 m) there are only 3 species. In the western tropics around Guyana the disparity is 7 shelf-species (Altena, 1968; Moore, 1977) and 4 abyssal species. In the temperate western Atlantic there are 4–5 shelf species (Mighels & Adams, 1842; Hampson, 1971; Abbott, 1974) as compared with 5 abyssal species in the North America Basin. The reduction in nuculid diversity with increasing depth in the north east and tropical west Atlantic may be related to the fact that 'crenulate' species were not present in shallow water before the Cretaceous and therefore only comparatively recently have they invaded the deep sea.

DISCUSSION

The species described here are based on morphological characters and therefore would be regarded by numerical taxonomists as morpho-species rather than biological species as defined by Mayr, (1949). There is no biological reason why inability to interbreed should always be traceable to morphological differences (Savory, 1962), and classifications based on similarity alone may not always reflect genetic affinity. Nevertheless, the morphological differences between intra-basin species are sufficiently large to more-or-less exclude the possibility that they are variants of a single species. Widely distributed species such as *D. atacellana* with numerous populations as far apart as the Rockall Trough and the Argentine Basin (approximately 7000 miles) may turn out to be more than one species on the basis of, say, electrophoretic evidence. Overall the deep-sea bed is not subject to large amounts of environmental heterogeneity, consequently it is hypothesized that populations in this environment would maintain little genetic variability (Manwell & Baker, 1970; Grassle, 1972; Grassle & Sanders, 1973). In fact deep-sea species are far from genetically depauperate and may maintain levels of genetic variability which are average or above average for marine invertebrates (Gooch & Schopf, 1972; Ayala & Valentine, 1974; Valentine & Ayala, 1975; Ayala *et al.*, 1975; Murphy *et al.*, 1976), and have as much if not more potential for change as organisms from other environments.

Although the nuculids are preadapted for deep-sea existence (eg. feeding and shell composition) their life in deep water has been accompanied with adaptation. This includes reduction in the area of the gill and number of plates, the elongation of the hindgut, a reduction in the number of ciliated grooves in the stomach, an increase in egg size and a reduction of body size and low productivity. Probably all are adaptations to nutritional impoverishment but are also likely to be accompanied by physiological adaptation to low temperature and high pressure. Nevertheless, none of the Atlantic deep-sea nuculids can be regarded as truly abyssal since no species reaches an *optimal* population density at abyssal depths (ie. >4000 m). Only two species, *B. verrilli* and *D. atacellana*, have distributions which exceed 4000 m and both of these are also found at slope depths. Indeed, most species are restricted to the continental slope with diversity reaching a maximum between 1000–2000 m. Reduction in diversity as abyssal depths are approached is recorded in a number of macrofaunal groups (Sanders *et al.*, 1965; Rex, 1973, 1976) and may be a result of extremely low productivity at these depths. One adaptation to low productivity is the reduction of body size, but there must be a limit to this particular adaptation. Rex, (1973) suggests that productivity affects macrofaunal diversity only when the lower limit of adaptation in size is approached.

Co-existing protobranchs having closely similar feeding habits and apparently identical food in their guts has to be explained against the apparent lack of potential niches within the soft monotonous abyssal sediment. Originally 'niche' was defined as the subdivision of the environment within which the species lives (Grinnell, 1917). Hutchinson, (1957) reformulated the concept in terms of set theory such that if each environmental variable is given a co-ordinate in an N-dimensional space, then a niche can be defined as a multi-dimensional hypervolume in which the fitness of the individual is positive. Real separation of species may be based mainly on trophic rather than physical or chemical factors (Green, 1971), and this may well apply in the deep-sea where if protobranch niche demarcation does exist in the deep-sea environment, it appears to be very subtle, and may be a product of biochemical specialization and differing spatial requirements (Grassle & Sanders, 1973; Allen, 1983).

The distribution of cosmopolitan species such as *Deminucula atacellana* and *Nuculoidea subovata* seems to be attributable to the production of pelagic larvae. Species which have direct development, such as *Nuculoma similis* and *Nucula delphinodonta* have restricted distributions. Pelagic larvae of deep-sea protobranchs have never been collected from surface waters, therefore, transportation must take place in deep water. The velocity of deep-sea currents range from 1.5 to 44 cm/sec (Knauss, 1965; Webster, 1969; Schmitz *et al.*, 1970; Hogg, 1983; Saunders, 1983), and if the duration of larval transport is only a few days, larvae could in theory be transported many kilometres.

Pelagic larvae are not only important as a means of dispersal but also for maintaining genetic continuity. The lack of morphological differences between widely separated populations of *D. atacellana* and *N. subovata* suggest frequent genetic exchange between these populations and that long-lived larvae exist in the deep sea. Discontinuities in the distribution of deep-sea nuculids are difficult to explain but could be related to a dispersal controlled by prevailing currents and ridge systems.

The results of this study and that of Bouchet and Warén, (1979) show that none of the North Atlantic abyssal nuculid species occur north of the North Atlantic Transversal Ridge. Although both *D. atacellana* and *N. subovata* are common in the Rockall Trough, adjacent to the ridge, neither are found in depths less than 1000 m and it must be that their larvae are unable to travel north into the Norwegian Basin against the prevailing deep cold water currents originating in high latitudes (Lynn & Reid, 1968). There also appear to be no nuculids common to the abyss of both the Atlantic and the Antarctic (Soot-Ryen, 1951; Powell, 1960, 1965; Dell, 1964, 1972) even though there appears to be no barrier. The Cape Basin also appears to have few affinities with the rest of the Atlantic as far as nuculids are concerned. There are no species common to the Cape Basin and the adjacent Angola Basin, yet two species found in the Angola Basin are found in other Basins on both sides of the equator. Clarke, (1960) only found one nuculid species, *Pronucula benguelana*, in the Cape Basin, and neither this species nor the genus is found in any other Atlantic Basin.

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Notes on the anatomy and classification of ophidiiform fishes with particular reference to the abyssal genus *Acanthonus* Günther, 1878

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Synopsis. Although the dominant group of benthic deep-sea fishes, Ophidiiformes are virtually unknown anatomically. This study focuses on anatomical features of the abyssal genus *Acanthonus* a taxon which previous authors have considered specialised. Of *ca* 80 ophidioid and bythitoid genera, 36 have been utilised for comparative study. The characters investigated are those commented upon by previous authors and ones not previously described. Characters identified as synapomorphic are the hypertrophy of the RLA-PP (pelvic) nerves, divergence of the supraorbital trunk of the trigeminal nerve complex external to the trigeminal foramen, reduction and loss of epipleural ribs and posterior shift of the swimbladder. The distribution of these characters upholds the classification of Cohen & Nielsen (1978) with respect to the recognition of a monophyletic Brotulinae and Ophidiinae, but indicates that the Neobythitinae is paraphyletic with part (*Hypopleuron*) being the sister-group to other ophidioids and bythitoids and other parts being closely related to respectively, brotulines and aphyonids. The Bythitidae also appears non-monophyletic with respect to one genus, *Brosmophyciops* whose phylogenetic position is ambiguous. The majority of Neobythitinae and Bythitidae are considered as a monophyletic assemblage, the detailed relationships of which are yet to be ascertained. It is confirmed that *Acanthonus* possesses several autapomorphies, and synapomorphies which support Cohen & Nielsen's (1978) contention that its close relationship lies with *Tauredophidium* and *Xyelacyba*.

INTRODUCTION

Gosline (1953) noted the dearth of anatomical accounts of ophidiiform (brotulid) fishes, reiterated by Cohen (1974) and Cohen & Nielsen (1978). Nearly fifteen years on the situation remains almost the same; there is no broad comparative anatomical treatment of the group.

Gosline (1960) also drew attention to the size and heterogeneous nature of the group noting that 'known variation in osteological features in greater than between many families of . . . Percoidae'. In current systematic parlance this variation and heterogeneity can be attributed to an array of apomorphic features most of which appear to be autapomorphic at the generic 'level', witness the many (twenty-four among eighty-two [29%]) monotypic genera.

No attempt is made here to provide anything approaching a comprehensive anatomical survey of ophidiiform taxa, instead certain anatomical features are detailed from the standpoint of *Acanthonus*, a monotypic abyssal genus (Fig. 1). *Acanthonus* is presently placed in the majority ophidiiform group, the Neobythitinae; it appears to possess a number of specializations correlated with its abyssal life (Nielsen, 1966; Horn *et al.*, 1978) most of which appear to be unique but offering the possibility that some might be shared with anatomically uninvestigated taxa. It is these 'unique' features together with certain ophidiiform features commented upon by previous authors which are used as starting points in making a broader comparative anatomical investigation.

Regan (1903; 1912) and Gosline (1953) had made assertions concerning certain ophidiiform features and it is these which have been taken as a starting point for a broader comparative investigation. The taxonomic breadth of the comparisons is, however, limited by the availability of material. Among the *ca* eighty ophidioid and bythitoid genera, thirty-six (45%) have been used and then not for every character complex. By examining a combination of osteological, myological and neurological features it was hoped that synapomorphies would be revealed which would identify at least basal monophyletic assemblages. Thus far, only one potential synapomorphy, involving the morphology of the cranial articular facets and their connection with the vertebral column, has been recognised as splitting ophidiiforms into the Carapidae plus Ophidiidae and the Bythitoidei, the latter being the derived assemblage (Patterson & Rosen, 1989). Monophyly of the Carapidae has recently been satisfactorily demonstrated by Markle & Olney (1990) while that of both the Ophidiidae and Bythitoidei remains suspect.

METHODS AND MATERIALS

Although Patterson & Rosen (1989) recognised the Bythitoidei as a monophyletic group they were not explicit in the content of that group naming only certain genera lacking the synapomorphic 'cod-like' exoccipital facets and which were classed as 'ophidiids'. For the purposes of the anatomical descriptions the usage of 'ophidiiform(s)' embraces the Ophidoidei and Bythitoidei *sensu* Cohen & Nielsen (1978), the Carapidae being treated as an outgroup along with other paracanthopterygians.

Specimens examined (the majority have been dissected and radiographed and from some the cranium has been extracted): *Abyssobrotula galatheae* Nielsen Uncat. 'Discovery' Stn 10652, 5112 m (149 mm SL); *Acanthonus armatus* Gnthr 1990.8.21:78a–f (6 specs 290–350 mm SL), off Cape Verde, 3120 m; 1887.12.7.55 (holotype, 285 mm SL), Philippines; 1887.12.7.56 (Paratype, 310 mm SL) North of New Guinea; *Aphyonus gelatinosus* Gnthr 1887.12.7:59 (Holotype, 130 mm SL), N.E. Australia; *Barathrodemus cf. manatinus* Goode & Bean 1991.11.14.1 (107 mm SL), 24°25′N, 77°22′W; *Barathronus bicolor* Goode & Bean 1961.9.7:1 (104 mm SL), Puerto Rico; *Bathyonus* sp. Uncat. 'Discovery' Stn 12179 (190 mm SL); *Bassozetus taenia* (Gnthr) 1990.8.21:97–8 (205 mm SL, skull prep.), Cape Verde; *Bassozetus* sp. 1991.7.9:10–33 'Discovery' Stn 10884 (*ca* 156, 170 mm SL); *Brosmophyciops* sp. 1991.11.14:2 (52 mm SL) N.W. Gulf of Aqaba; *Brotula multibarbata* Temminck & Schlegel 1983.3.25:1128–30 (103 mm SL), Fiji; *Carapus acus* (Brunn.) 1952.11.25:1–4 (180 mm), Naples; *Carapus bermudensis* (Jones) 1985.6.6:138–183 (alizarin/alcian), Bimini; *Cataetyx* sp. 1990.8.21: 184–8 (226, 250 mm SL; skull prep.), Porcupine Seabight; *Cherublemma emmelas* (Gilbert) 1985.6.6:136–7 (205 mm SL), Baja California; *Dicrolene intronigra* Goode & Bean 1939.5.24:1441–4 (135 mm SL), S. Arabian coast; *Dinematichthys* sp. 1983.3.25:1123–5 (92 mm SL), Fiji; *Diplacanthopoma brachysoma* Gnthr 1972.10.24:4 (185 mm SL) 9°03′N, 81°18′W; *Echiodon drummondii* Thompson 1969.5.4:3–5 (300 mm SL) 58°N, 9°W; *Genypterus blacodes* (Schneider) 1936.8.26:1052–7 (290 mm SL) S. Atlantic; 1896.6.17:73, (skeleton) Melbourne Market; *Glyptophidium macropus* Alcock 1939.5.24:1458–65 (170 mm SL, skull prep.) Gulf of Aden; *Hoplobrotula armata* (Temminck & Schlegel) 1938.6.23:27–8 (193 mm SL), Chousi, Japan; *Hypopleuron caninum* Smith & Radcliffe 1986.10.6:63–65 (330 mm SL) Indonesia; *Lamprogrammus fragilis* Alcock 1939.5.24:1493–6 (130 mm, body truncated: 220 mm SL) S. Arabian coast; *L. niger* Alcock 1939.5.24:1483–7 (300 mm SL; skull ex *ca* 380 mm SL) maldive area; *Lepophidium profundorum* (Gill) 1984.8.8:263–6 (105 mm SL) Baja California; *Lucifuga dentatus* Poey 1981.10.27:1–4 (104 mm SL) Cuba; *Monomitopus metriostoma* (Vaillant) 1964.8.6:47–54 (135 mm SL) 7°55′N, 12°38′E; *Neobythites gilli* Goode & Bean 1967.11.9:1–6 (100 mm SL) Caribbean; *N. steatiticus* Alcock 1910.1.31:11 (skeleton) Sea of Oman; *Nybelinella erikssoni* (Nybelin) 1991.5.7:2 (58 mm SL) 'Discovery' Stn 11261, 5440 m; *Ogilbia cayorum* Evermann & Kendall 1985.6.6:128–135 (69, 72 mm SL) Bahamas; *Ophidion rochei* Muller 1971.12.17:6–8 (175 mm SL) and Uncat. (170 mm) Black Sea; *Penopus* sp (285 mm SL) 'Discovery' Stn 12177 (No. 2); *Petrotyx sanguineus* (Meek & Hildebrand) 1976.7.15:205 (410 mm SL) B.V.I.; *Porogadus trichiurus* (Alcock) 1939.5.24:1453–5 (175 mm SL) Zanzibar; *Pycnocraspedum squamipinne* Alcock 1939.5.24:1497–8 (114 mm SL) Zanzibar; *Sirembo imberis* (Temminck & Schlegel) 1905.2.4:450–4 (137 mm SL; skull prep.) Wakanoura, Japan; *Spectrunculus grandis* (Gnthr) Uncat. (125 mm SL, alcian stained spec.) 'Discovery' Stn 51015, 2540 m; 1990.8.21:106–111 (420; 250; 220 mm SL, skull prep) Porcupine Seabight; *Tauredophidium hextii* Alcock 1890.11.28:38 (type, 100 mm SL) Ganjam Coast; 1992.2.4:3–5 (89 mm SL) 11°31′S, 86°55′E; *Thalassobathia pelagica* Cohen 1967.11.8:1 (240 mm SL) Donegal; *Typhlonus nasus* Gnthr 1887.17.7:58 (Holotype, 205 mm, tail missing) N. of Celebes; 1887.12.7:587 (Paratype, 215 mm SL) N.E. of Australia; 1992.2.4:6 (190 mm SL) Indian ocean; *Xyelacyba myersi* Cohen USNM 320096 (120 mm SL) 24°51′N, 90°00′W; USNM 212087 (73 mm SL) 38°35′N, 72°23′W; 1992.2.4:1–2 (170 mm SL) 25°S, 88′E.

Pediculati: *Antenharius nummifer* (Cuvier) 1888.12.29:143 (skeleton); 1898.12.24:103–112 (49 mm SL) Persian Gulf; *Porichthys porosissimus* (Val.) 1937.9.30:163–7 Bahia Blanca; 1890.11.15:150 (skeleton); *Lophius piscatorius* Linn.

1970.2.17:630–2 (95 mm SL) S.W. Ireland; Uncat. (skull).

Abbreviations used in the figures

A1,2,a,b	Divisions of *adductor mandibulae* muscle
aa	anguloarticular
ahf	anterior hyomandibular fossa
asp	autosphenotic
bl	Baudelot's ligament
blf	fossa for attachment of Baudelot's ligament
bo	basioccipital
boc	basioccipital cavity for articulation with first centrum
bof	basioccipital facet
c	centrum (numbered)
c1p	anterior process of first centrum
cc	cerebellar corpus
cl	cleithrum
cle	cleithral extension
cs	spinal cord
de	dentary
do	*dilatator operculi* muscle
dRLA	dorsal branch of ramus accesorius lateralis nerve
dsp	dermosphenotic
ect	ectopterygoid
ent	entopterygoid
epd	dorsal epaxial muscle
epl	anterior lateral segment of *epaxialis* muscle
epm	anterior medial segment of *epaxialis* muscle
epo	epioccipital
epr	epipleural rib
eps	lateral band of epaxial muscle connecting 1st and 4th ribs
epx	epaxial muscle
es	ethmoid spine
exc	exoccipital condyle
exf	exoccipital facet
exo	exoccipital
fc	frontal crest
fg	foramen for glossopharyngeal nerve
fh	foramen for hyomandibularis nerve
fli	lateral ethmoid-first infraorbital facet
flp	lateral ethmoid-palatine facet (lateral)
fm	foramen magnum
fmp	lateral ethmoid-palatine facet (medial)
foo	foramen for optic-olfactory and trigeminal nerves
fon	foramen for occipital nerves
fr	frontal
fRLA	foramen for ramus lateralis accessorius nerve
fsn	spinal nerve foramen
ft	facial trunk of trigeminal nerve
fv	vagus nerve foramen
ga5	5th gill-arch
hb	hyoideus branch of hyomandibularis nerve
hy	hyomandibular
hyb2	2nd hypobranchial
hyx	hypaxial muscle
ic	intercalar
ica	*infracarinalis anterior* muscle
ih	interhyal
io	interoperculum
ki	kidney
lal	labial ligament
lap	*levator arcus palatini* muscle
lc	compound ligament
lcc	part of compound ligament connecting swimbladder with first rib
le	lateral ethmoid
lei	ethmoid-infraorbital ligament
li	liver
lin	interneural ligament
lmi	mandibular-interopercular ligament
lnr	neural-rib ligament
lo	*levator operculi* muscle
lpo	preopercular-opercular ligament
lpv	palato-vomerine ligament
lsv	swimbladder-vertebral ligament
mb	mandibular branch of hyomandibularis nerve
mbo	outer subbranch of above
me	mesethmoid
mec	ethmoid cartilage
med	medial opening of mandibular canal (dentary)
mt	metapterygoid
mx	maxilla
nI-X	cranial nerves
na1	first neural arch
na2	second neural arch
nad	auditory nerve
nmd	mandibular branch of trigeminal nerve
nmx	maxillary branch of trigeminal nerve
ns	neural spine
nv	vagus nerve
of	olfactory foramen
ofb	olfactory bulb
ofl	olfactory lobe
on	notch in lateral ethmoid for olfactory nerve
onp	perforation in orbital septum for olfactory nerve
op	operculum
opl	optic lobe
os	orbital septum
pal	palatine
pap	palatine prong
par	parietal
pb	pelvic bone
pce	*pharyngoclavicularis externus* muscle
pcl	postcleithrum
pe	peritoneum
ph	posterohyal
phy	*pharyngohyoideus* muscle
plr	pleural rib
pm	pelvic muscles
pmr	medial ridge of parasphenoid
pmx	premaxilla
ppf	posterior (pterotic) hyomandibular fossa
pr	pelvic fin ray
pro	prootic
ps	parasphenoid
psp	parasphenoid process
pte	pterotic
pts	pterosphenoid
ptt	posttemporal
q	quadrate
r1	first enlarged rib (pleural or epipleural)
r2,3	ribs (pleural or epipleural)
ra	retroarticular
rc	rostral cartilage
rd	*retractor dorsalis* muscle
rds	rostrodermosupraethmoid

RLA-PEL	pelvic branch of RLA nerve
RLA-PP	pectoral-pelvic branch of RLA nerve
rm	recti muscles
sb	swimbladder
sbc	sclerified cap of swimbladder
shl	lateral segment of *sternohyoideus* muscle
shm	medial segment of *sternohyoideus* muscle
smx	supramaxilla
sn	spinal nerve
so	supraoccipital
sol	semi-ossified ligament
sop	suboperculum
sot	supraorbital trunk of trigeminal nerve
sp	sphenotic
ste	sclerified tunica externa of swimbladder
sy	symplectic
tepm	tendon of medial epaxial (swimbladder) muscle
ti	tunica interna
tnp	perforation in orbital septum for trigeminal trunk
uh	urohyal
ut	tendon-ligament connecting *sternohyoideus* with urohyal
vh	ventrohyal
vo	vomer
vps	vertebral parapophysis
vsr	ramus of third spinal nerve
vvp	vertebral ventral process

ANATOMICAL FEATURES

Ethmo-vomerine region and palatine

In *Acanthonus* the ossified dorsal surface of the ethmoid (rostrodermosupraethmoid, RDS) is produced anteriorly into a broad, dorsally channelled strut with a bifurcate tip which pierces the skin (Figs 1;2): this is the bifid spine referred to by Cohen & Nielsen, (1978:18). The posterior border of the RDS is only partially overlain by the frontals. The anterior surface of the underlying ethmoid is sharp-edged and overlies a thick ethmoid cartilage which is visible only laterally (emc, Fig. 2). The lateral ethmoid (le, Fig. 2) is broad with a sloped anterior face abutting the mesethmoid cartilage and a thin lateral wing. The ventrolateral surface of the lateral ethmoid bears a well-developed almost vertically directed medial (fmp) and a weak laterally directed articulatory process (flp, Fig. 2). These processes articulate respectively with the medial and anterior surfaces of the palatine prong. The medial part of the lateral ethmoid is deep and contacts the parasphenoid ventroposteriorly and the frontal dorsally. Each lateral ethmoid is separated from its partner in the midline. The olfactory foramen is variously developed. In the specimen illustrated the 'foramen' appears as a notch on the posterior rim of the lateral ethmoid wing. The olfactory nerve merely passes over the edge of the bone and crosses its anterior face to where the olfactory rosette is situated. In other specimens a thin posterior stem of bone provides either a complete or incomplete closure of the notch. The vomer (vo, Fig. 2) has a deep and broadly triangular head and a short narrow shaft the posterior tip of which lies in line with the posterior borders of the lateral ethmoids. The tooth-patch is deep and the conical teeth are directed not only ventrally but also anteriorly and anterodorsally (Fig. 2C).

The ethmovomerine region of *Acanthonus* differs most noticeably from the other ophidiiform taxa examined in three respects, 1) elongation and bifurcation of the RDS; 2) position of the palatine articulatory facets on the underside of the lateral ethmoid; 3) disposition of the vomerine teeth.

As in *Acanthonus* in nearly all other taxa the anterior of the mesethmoid capping the ethmoid cartilage slopes forward. However, the slope is variable from being almost vertical (*Ophidion* and *Genypterus*; Fig. 3A) to shallowly sloped (*Cataetyx* and *Lamprogrammus*; Fig. 3F). In *Glyptophydium*

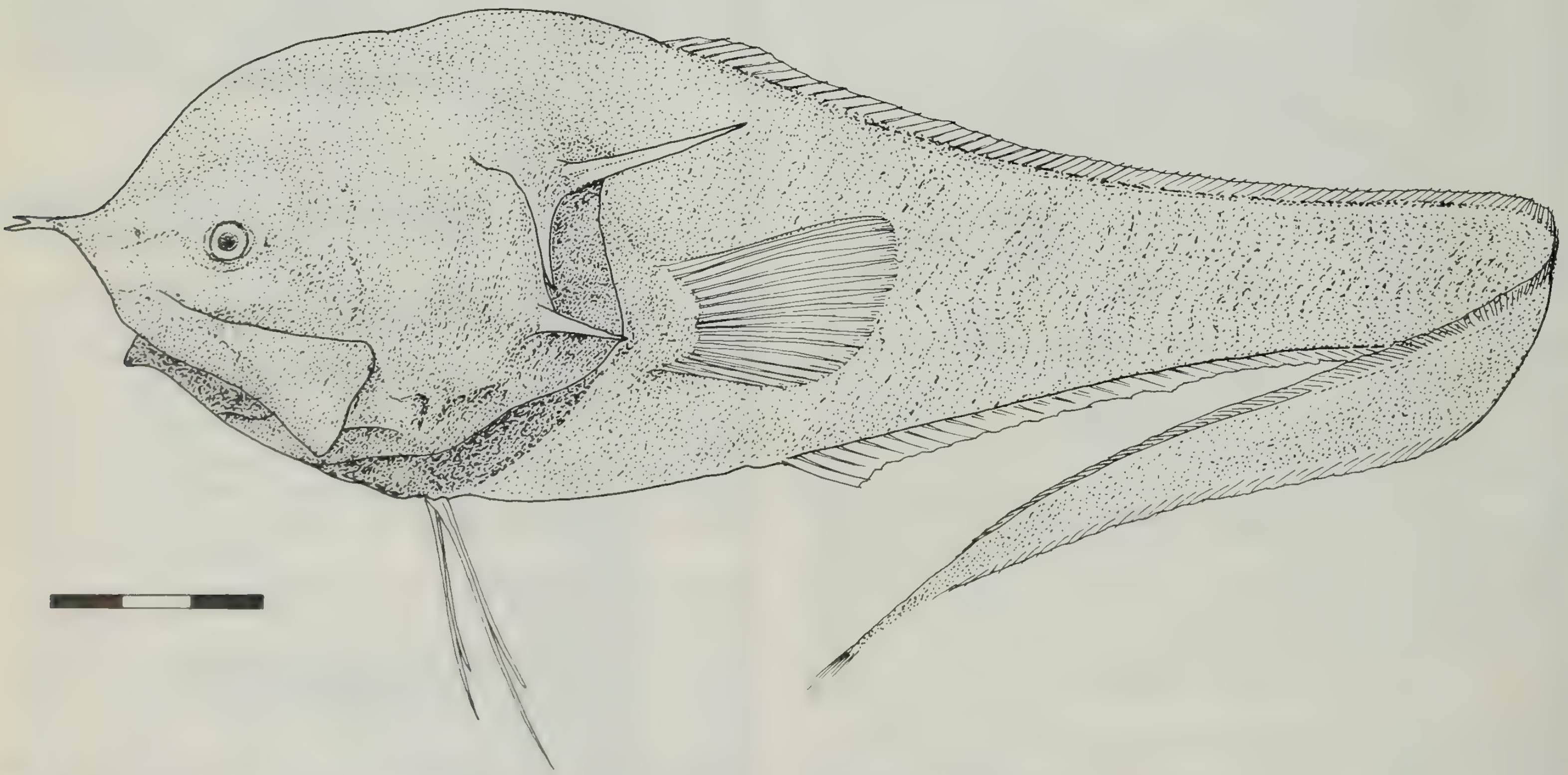

Fig. 1 *Acanthonus armatus*, life appearance based on type specimens, photograph in Horn *et al.* (1978) and Winther's drawing in Nielsen (1966). Scale in cms.

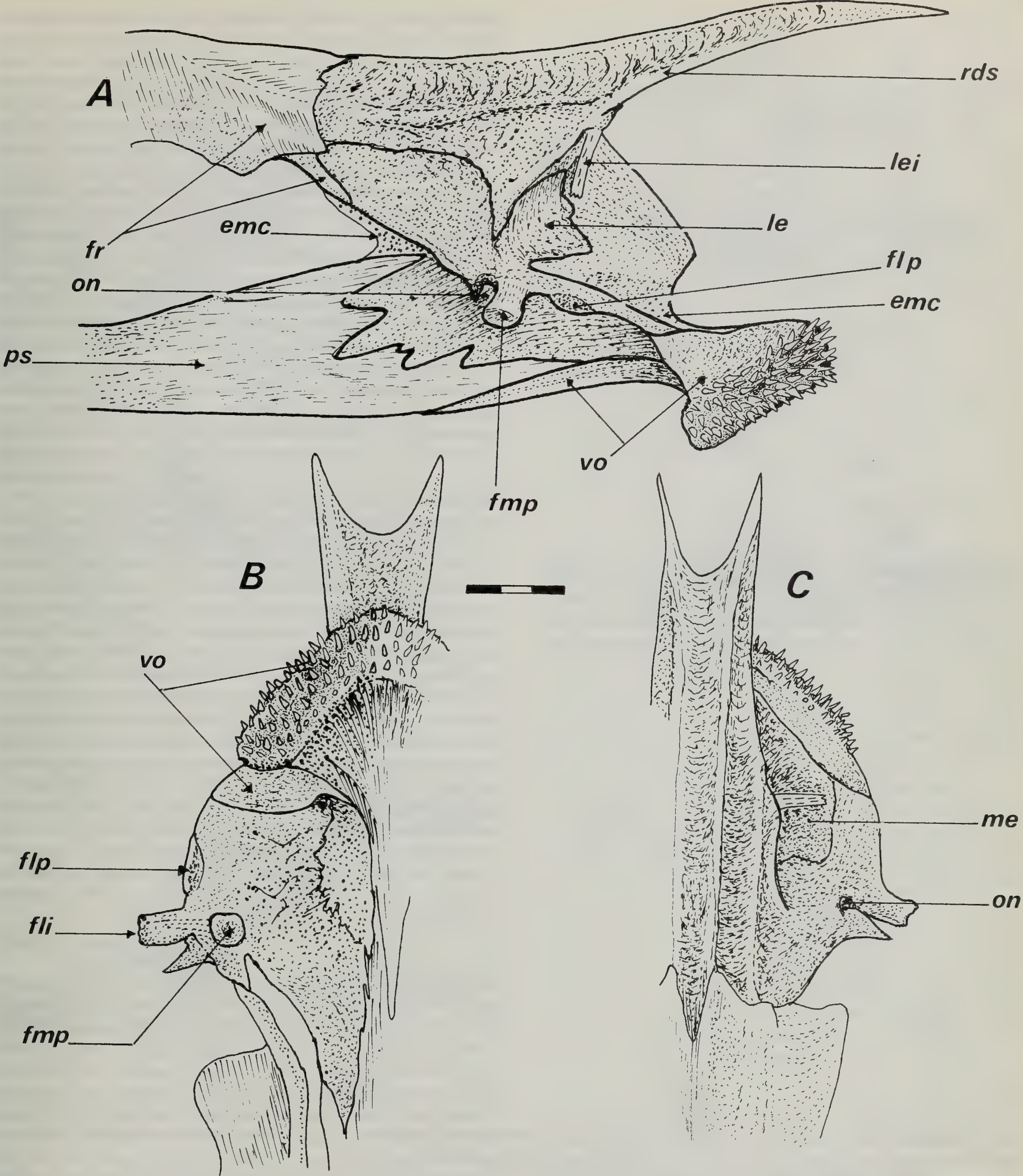

Fig. 2 *Acanthonus armatus* ethmovomerine region in A, lateral, B, ventral and C, dorsal views. Scale in this and subsequent figures in mm divisions.

(Fig. 3C), *Sirembo* and *Spectrunculus* the ethmoid region is indented and, notably in the latter genus, the frontals extend far anteriorly rising medially to form a crest which in *Glyptophidium* (Fig. 3C) is particularly pronounced. *Hoplobrotula* and *Tauredophidium* are the only other taxa examined which possess an anteriorly extended RDS spine (also reported by Machida, 1990). Only *Cataetyx, Brotula, Glyptophidium* and *Lamprogrammus* have a prominent lateral wing on the lateral ethmoid. In other taxa, including *Acanthonus*, the wing is feebly developed but always has a lateral facet which articulates with the first infraorbital (fli, Fig. 3).

The disposition of the palatine articulatory facets on the lateral ethmoid is a variable and perhaps important classificatory feature. Unlike the condition in *Acanthonus* where the

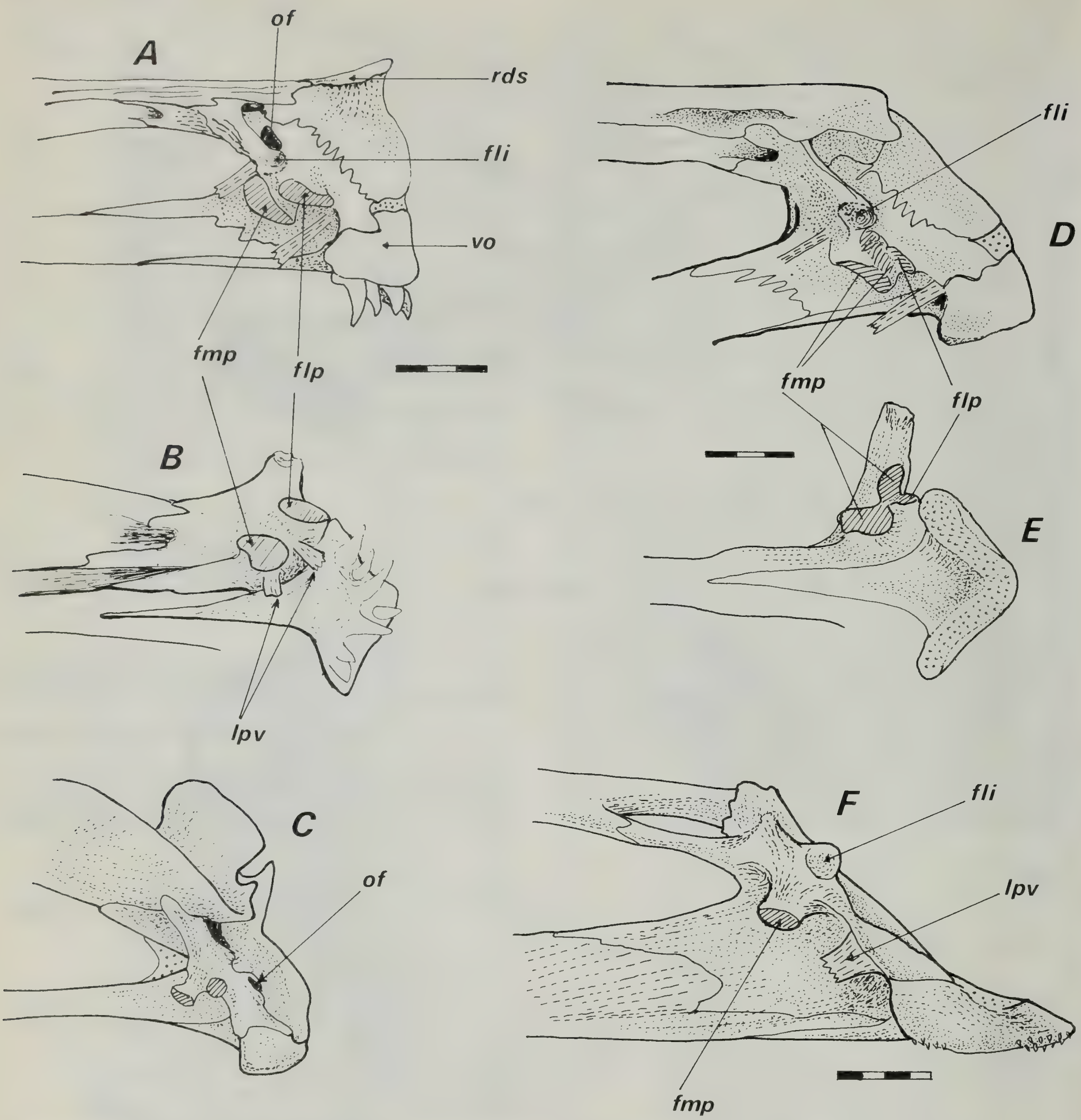

Fig. 3 Ethmovomerine regions of A and B *Genypterus blacodes* in lateral and ventral views; C, *Glyptophidium macropus* (lateral); *Brotula multibarbata* in D, lateral and E, ventral views; F, *Lamprogrammus niger* (lateral).

lateral facet is reduced, in other taxa examined both facets are equally well-developed. In *Brotula* (Fig. 3D,E), *Genypterus* (Fig. 3A), *Ophidion, Bassozetus, Glyptophidium* (Fig. 3C) and *Spectrunculus* the medial facet is large and ventroposteriorly directed and the outer facet is usually narrowly but clearly separated by a well-defined depression (exceptionally in *Brotula* the outer facet is juxtaposed to the inner and is continued on to the lateral flange of the lateral ethmoid; Fig. 3E). The lateral facet lies on the outer rim of the lateral ethmoid and is angled downward. The facets contact apposing surfaces on the palatine head, the medial articulating with the dorsomedial surface of the head, the lateral with the base of the palatine prong. In *Lamprogrammus* there is only a medial facet, the base of the palatine prong being attached to the lateral ethmoid rim by a thick ligament (Fig. 3F). In *Cataetyx* the facets lie in an almost straight line but are well-separated.

The palatine-lateral ethmoid articulation in *Acanthonus* is rigid and the leading edge of the palatine is tightly juxtaposed to the vomer so that the vomerine and palatine teeth are contiguous (Fig. 4B). A particular feature of the palatine teeth in *Acanthonus* is their lateral placement (Fig. 4B); in all other taxa examined the tooth patch is orientated along the medial surface of the bone so that nearly all the teeth point inward and only a single row is usually visible along the ventral margin of the bone. The palatine is secured to the lateral ethmoid by two ligaments (present in all taxa examined), one running from the dorsal indentation of the head of the bone or its medial rim to the lateral ethmoid wall, the other, which may sometimes be divided, from the inner face of the palatine prong to the lateral ethmoid cavity above the vomer (1pv, Fig. 3B). The latter ligament corresponds to Stiassny's (1986) anterior palato-vomerine ligament (VI). In all the taxa examined which embrace Cohen & Nielsen's (1978) brotulines, ophidines and neobythitines, this ligament invariably stems from the lateral ethmoid itself rather than the vomer. A medial palato-lateral ethmoid ligament is a widespread teleostean feature. There is, however, no posterior palato-vomerine ligament (Stiassny's ligament V) in any of the examined taxa. This absence is most likely a secondary loss associated with the development of lateral ethmoid-palatine articulatory facets.

The shape of the palatine, the angle at which the prong is directed and the proximity of the anterior palatine margin to the vomer are largely dictated by the orientation of the palatine facets with the corresponding articular surfaces of the lateral ethmoid. Usually the articulatory facets of the palatine are discrete, the medial one forming a right-angle to that on the neck of the prong so that the base of the prong lies in the saddle of the articulatory processes. As noted above, in *Cataetyx* the articulatory facets on the lateral ethmoid lie nearly in tandem, consequently the palatine prong extends directly forward rather than pointing ventrolaterally and the anterior lateral ethmoid facet appears to act as a stay. In its rigidity with the lateral ethmoid and juxtaposition with the posterior rim of the vomer, the palatine articulation of *Cataetyx* most closely approaches that of *Acanthonus* (Fig. 4A). There are, however, noticeable differences between the two taxa in the angle of the palatine prong and shape of articulatory surfaces which suggest that the resemblances have been independently derived.

Palatine-lower jaw bite

The reason for the rigidity of the palatine-ethmovomerine connection in *Acanthonus* becomes clear when it is realised that the palatine occludes with the lawer jaw (Fig. 4B). The palatine tooth patch is long, 75% of the dentary and when occluded the posterior tips of the palatine and dentary tooth-patches coincide (Fig. 4B). In other ophidiiforms (and indeed, other teleosts) there is no or only partial (see below) occlusion between the palatine and lower jaw; the length of the palatine tooth patch is usually only half that of the dentary and the teeth are angled medially and fall inside the lower jaw when the mouth is closed so that teeth are rarely visible in lateral view (Fig. 5C). To what extent, in life, the palatine can be rotated laterally so as to occlude with the lower jaw is not clear merely from the manipulation of the jaws of preserved specimens but certainly the connection between the palatine and ethmovomerine region is loose enough to allow some lateral rotation.

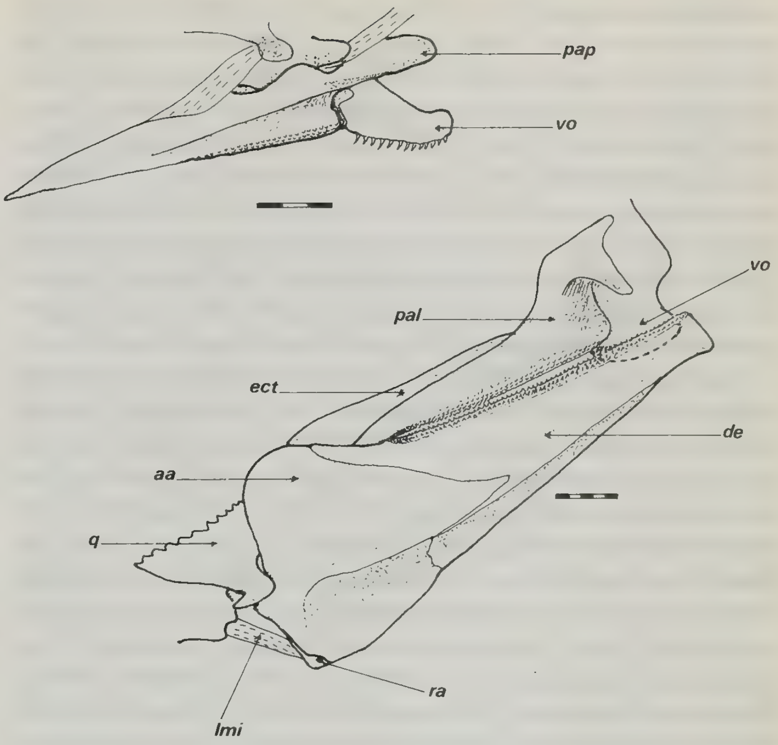

Fig. 4 Above, palatine and vomer of *Cataetyx* sp. (right lateral); below, palatine-lower jaw occlusion in *Acanthonus armatus*; the lower jaw is shown in the closed position and the elements are orientated with respect to the vertebral axis. Dashed outline indicates hidden border of the vomer.

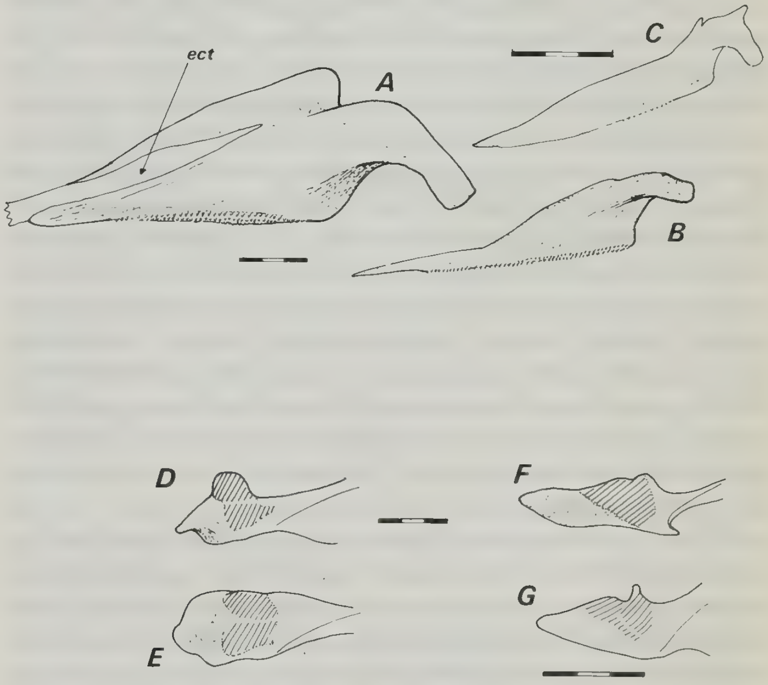

Fig. 5 Above, palatines of A, *Lamprogrammus niger*, B, *Spectrunculus grandis*, C, *Neobythites steatiticus* (right lateral views). Below, articulatory surfaces of lower jaws of D, *Acanthonus armatus*, E, *Lamprogrammus niger*, F, *Genypterus blacodes*, G, *Spectrunculus grandis* (dorsal view, medial surface at top).

Of the four exceptions among examined taxa two display partial and two (apparently) complete occlusion between the palatine and dentary. In *Lamprogrammus* and *Spectrunculus* only the posterior half of the palatine is in direct contact with the lower jaw when the mouth is tightly shut, the anterior half curving medially. The dentigerous surface of the palatine in *Spectrunculus* is longer than that of other taxa (Fig. 5B) but nonetheless its posterior tip extends backward beyond the posterior tip of the dentary tooth patch, a feature common to all other genera examined. In both *Lamprogrammus* and *Spectrunculus* the palatine dentigerous area is exposed laterally (Figs 5A & B). From radiographs and partial dissections of *Tauredophidium* and *Xyelacyba* it would seem that these taxa also have complete or nearly complete occlusion of the palatine and lower jaw. In *Xyelacyba* the palatine is deep with a strong and steeply angled prong (as in *Acanthonus*) and in both *Tauredophidium* and *Xyelacyba* the palatine tooth patch is narrow with the teeth laterally exposed.

Acanthonus is not unusual among ophidiiforms in lacking upper and lower jaw occlusion, indeed it seems to be the common condition among this group of fishes that the lower jaw is surrounded by the upper when the mouth is shut. The feature is most clearly seen in *Spectrunculus* where the rather sharp-edged lip of the lower jaw forms a tight seal with the overlapping upper lip. *Typhlonus* is unusual among ophidiiforms in possessing long premaxillary ascending processes which also allow the upper jaw to envelope the lower. The dentigerous surface of the upper jaw rarely contacts that of the lower although in *Cataetyx* the tooth bands contact one another anteriorly. In *Lamprogrammus* there is a prominent dentary symphyseal process which lodges in a symphyseal notch in the upper jaw and although *Acanthonus* also bears a similar dentary process it is completely covered when the upper jaw is closed.

Quadrate-preopercular modification

The occlusion between the palatine and lower jaw teeth in *Acanthonus* is allowed principally by modifications in the relationship of the quadrate to the lower jaw and the contact between the quadrate and preoperculum. *Acanthonus* differs principally from other taxa examined in having the quadrate outwardly curved and the arc of that curvature continued through the ectopterygoid thus considerably displacing the palatine laterally (Fig. 6). In other ophidiiform taxa the anterior border of the quadrate is either perpendicular or inwardly curved so that the palatine lies either in the same vertical plane as the quadrate condyle or only slightly laterally (Fig. 6). Only in *Spectrunculus* is there a noticeable outward curvature of the quadrate and lateral displacement of the palatine. The shape of the *Acanthonus* quadrate condyle shows no special modification although it is somewhat shallower and its medial face more attenuated ventromedially than that of other taxa (Fig. 6).

When the lower jaws of various taxa are positioned at the same angle with respect to the quadrate it is seen that in *Acanthonus* the upper anterior face of the bone and the lower border of the ectopterygoid are obscured laterally by the anguloarticular; in the other taxa, there is a wide separation between the quadrate-ectopterygoid border. Only *Lamprogrammus* approaches *Acanthonus* in the separation of the elements (radiographs of *Tauredophidium* indicate a similar condition). *Acanthonus* and *Lamprogrammus* also possess a similarly modified anguloarticular condyle and its shape possibly dictates the alignment of the lower jaw (the condition in *Tauredophidium* is unknown). In the majority of ophidiiform taxa examined the anguloarticular is elongated, terminating in a posteriorly directed pointed or rounded process (Figs 5F & G). The transverse saddle of the condyle is well defined and the articulatory surface is elongate and extends on to the medial side of the condyle. In contrast both *Acanthonus* and *Lamprogrammus* have a short articulatory condyle with an angled, slightly upturned blunt posterior process and there is a well-defined saddle with articulatory facets equally or nearly equally disposed on either side (Figs 5D & E).

The articulation between the ventral surface of the quadrate and the lower limb of the preoperculum in *Acanthonus* is absent in the majority of other taxa examined. The posteroventral surface of the quadrate is flared and sits across a similarly widened preopercular flange (Fig. 7). A preopercular flange, which extends ventrally to cover the neuromasts, is common to all the taxa examined but in *Acanthonus* it extends shelf-like from the bone and terminates in a ventrally extended triangular process (Fig. 7). *Lamprogrammus* and *Xyelacyba* also have a broad based quadrate and an extended preopercular lateral flange (radiographs of *Tauredophidium* indicate a similar condition). In *Lamprogrammus*, however, the flange does not turn ventrally but extends laterally well beyond the quadrate border. *Acanthonus* differs from all these taxa in that it is only the posterior half of the quadrate which contacts the preopercular limb. In the others nearly the entire quadrate lies on the preopercular limb so that its anterior tip comes close to the quadrate condyle.

In *Acanthonus* the preoperculum has a slender upright limb which has a slight anterior ridge and a short horizontal limb (Fig. 7). In addition to the lateral ventral spine (see above) the posteroventral border is also produced into a long stout spine. In other examined taxa there are two principal conditions of the preopercular upright limb, it is either slender as in *Acanthonus* or short and broad with a rounded posteroventral margin. In those six taxa with a slender limb, five (*Neobythites, Hoplobrotula, Monomitopus, Dicrolene* and *Tauredophidium*) have the posteroventral border developed into two or three spines. *Tauredophidium* has especially long spines similar to those of *Acanthonus*. *Brotula* lacks preopercular spines and most of the lateral face of the upright limb is covered by a pronounced flange; the horizontal limb is also elongated and modified (see p. 122). Of those taxa with short, rounded upright preopercular limbs none bear spines but an anterior groove and flange is often present. In the taxa with a slender preopercular limb neuromasts are poorly developed but in those with a short limb are either moderately or well-developed (*Lamprogrammus, Dicrolene, Monomitopus*) or absent (*Genypterus, Cataetyx*).

A particular feature of *Acanthonus* is a ligament which stretches from the posterodorsal rim of the preoperculum across the hyomandibular articulation to the anteroventral margin of the operculum (lpo, Fig. 17); this feature is otherwise present only in *Tauredophidium* and *Xyelacyba*. In *Typhlonus* a strong ligament extends from a groove in the centre of the lateral face of the preoperculum to insert on the lower articulatory margin of the operculum and does not extend across it.

Hyomandibular articulation and foramina

In *Acanthonus* the hyomandibular is short, lacks a pronounced stem and has a slightly indented anterior margin and a short opercular articular process (hy, Fig. 7). The posterodorsal part of the bone has an acute mesad slope so that the perpendicular plane of the body and stem of the bone comes to lie at some distance lateral to its articulation with the cranium. The posterior half of the dorsal border of the hyomandibular curves sharply mesad so that the posterior

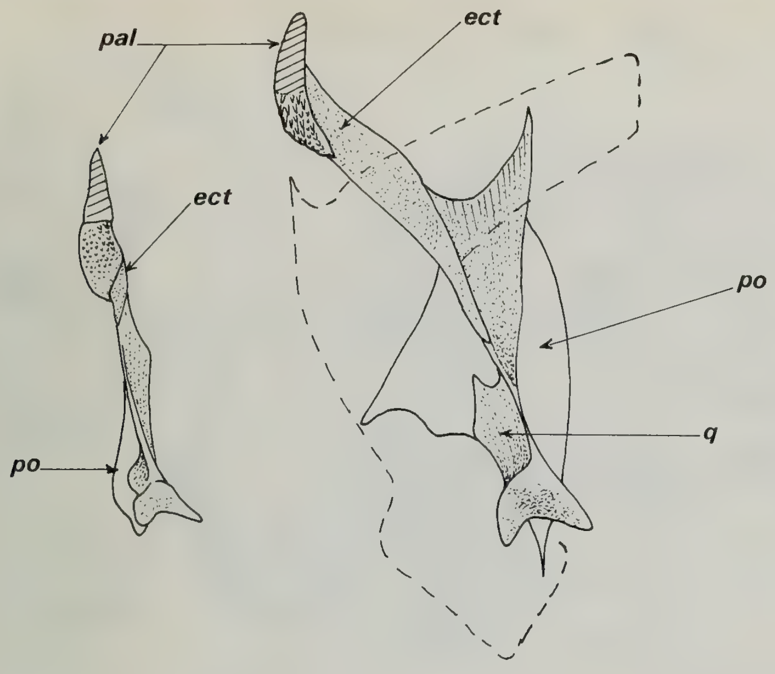

Fig. 6 Palato-pterygoid orientation right side, viewed anteriorly, in *Acanthonus armatus* (right) and *Neobythites steatiticus* (left). The anterior part of the palatine has been cut through (hatched). The position of the lower jaw in *Acanthonus* is shown by a dashed line.

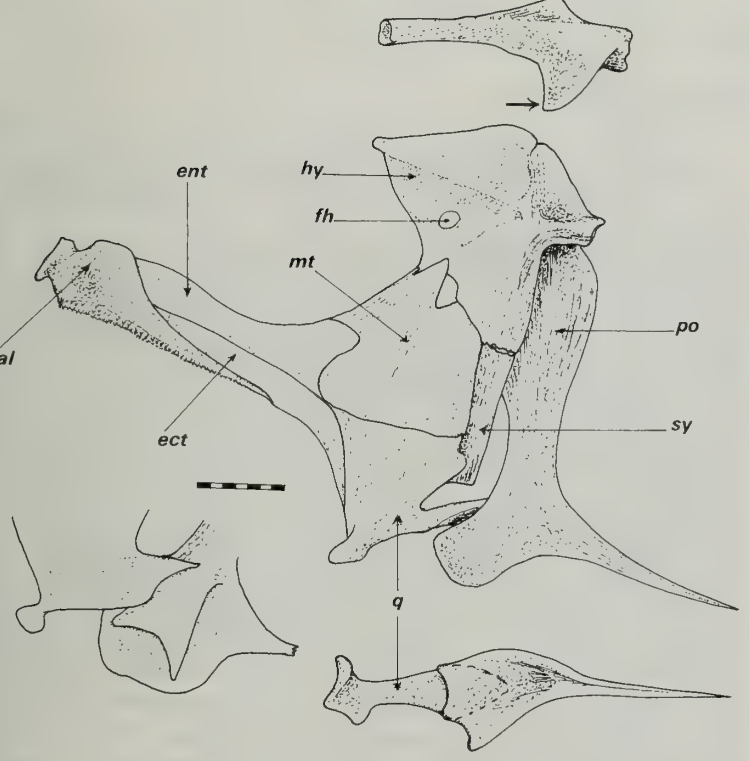

Fig. 7 *Acanthonus armatus*; hyomandibular and palato-pterygoid series, right side, in medial view (main figure); above, dorsal view of hyomandibular, medial surface to the bottom, the arrow indicates the surface articulating with the pterotic; below, ventral view of quadrate and preoperculum (dashed line shows shape of quadrate base), lateral surface at top; below left, lateral view of quadrate showing its contact with the preoperculum.

articulation is with a shallow fossa which curves around the posterior border of the pterotic and terminates in a notch (ppf, Fig. 8). The anterior articulation is with a deep fossa on the posterior surface of the sphenotic. The anterior fossa extends posteriorly as a shallow groove a short way along the pterotic and is widely separated from the posterior fossa (ahf, Fig. 8).

The foramen for the hyomandibular trunk of the facial (VII) nerve lies in the centre of the anterior field of the bone and the nerve passes directly through it to immediately turn ventrad on the lateral face. In no other ophidiiform taxon examined does the upper part of the hyomandibular curve mesad as in *Acanthonus* and in only three genera (*Spectrunculus, Bathyonus, Bassozetus*) is the nerve foramen situated in the anterior field. In other taxa the foramen perforates the dorsoanterior strut of the bone. The nerve enters a medial opening and courses posteroventrally through the strut to exit from a lateral opening situated at a lower level than the medial (Figs 9B & C). Markle & Olney (1990) report that in *Brotula multibarbata* the hyomandibular foramen is small and located close to the edge of the bone. Furthermore, they note two conditions of the foramen in carapids whereby it either pierces the anterior strut or the area below the strut. These conditions correspond to the two states observed in ophidioids. Markle & Olney's observation of a small, anteriorly located foramen in *Brotula* is either erroneous or based on an aberrant specimen (in their figure (24) the foramen seems too small to transmit the large diameter trunk of the hyomandibular nerve). As such their polarity assignment of a derived state to the larger carapid foramen is questionable.

A foramen piercing the hyomandibular anterior strut appears to be the widespread euteleostean condition since it occurs in virtually all of a wide range of taxa examined (clupeomorphs, ostariophysans, berycoids, atherinomorphs, percomorphs). Among other paracenthopterygians the hyomandibular has been modified to a greater or lesser extent with subsequent relocation of the foramen and nerve course. In gadiforms attrition of the anterior strut has resulted in the foramen appearing at the anterior margin of the hyomandibular rather than the medial face of the bone (Howes, 1989), a character which Gosline (1968) used to define Gadiformes. In the bathygadid *Gadomus* attrition of the anterior strut has led to complete absence of an anterior hyomandibular foraman, a feature also common to (?all) macrouroids (Howes, 1989, figs 8 & 9A). Interestingly, the absence of a dorsoanterior strut from the hyomandibular of *Acanthonus* suggests a direct correlation with the loss of the pars jugularis. In the pediculate paracanthopterygians examined (*Lophius, Antennarius, Porichthys*) the hyomandibular trunk travels through the central stem of the bone (Fig. 9A) and upon exiting *via* a lateral foramen at the base of the stem the hyoideus branch departs from the mandibularis branch. In gadiforms the hyoideus departs from the mandibularis prior to entering the hyomandibular and travels separately within or across the bone (Howes, 1989, Fig. 9). In ophidiiforms and other teleosts examined the hyoideus branch departs from the mandibularis immediately on leaving the foramen and crosses the lower face of the hyomandibular (Fig. 9C). *Brotula* is unique amongst the ophidiiforms examined in that the hyoideus branch runs interiorly through the stem of the hyomandibular before exiting posteroventrally (Fig. 9B).

The 'precursor' of the *Brotula* condition occurs in *Hoplobrotula* where a strong flange lies diagonally along the lateral face of the hyomandibular following the line of the central stem and partially covering the nerve. The conditions in *Brotula* and the pediculate paracanthopterygians are clearly not homologous since in the former only the hyoideus branch of the hyomandibular trunk runs internally and exits from a separate foramen. The Pediculati are derived with respect to

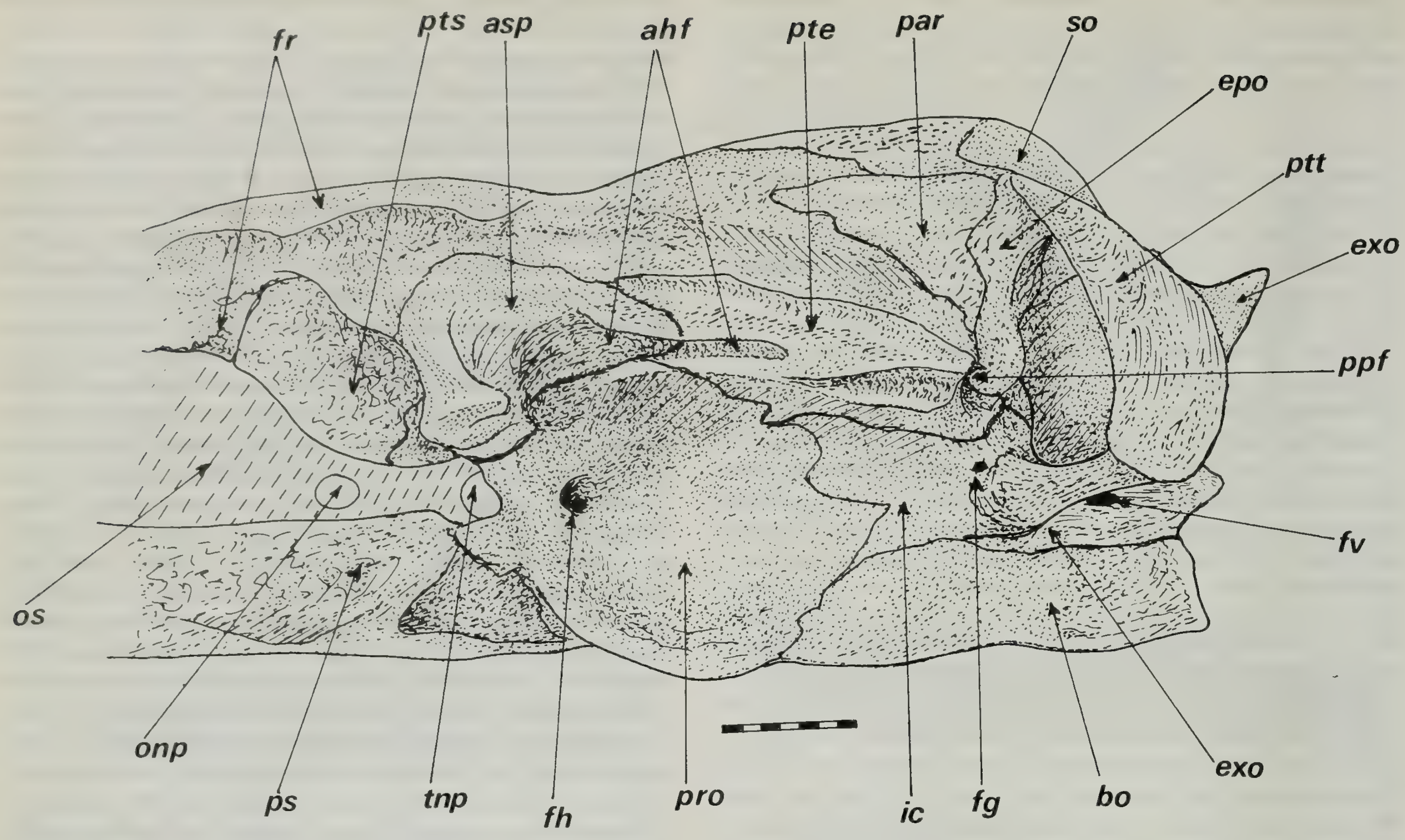

Fig. 8 *Acanthonus armatus* Neurocranium; postorbital and occipital regions in left lateral view.

other Gadoidei in the enclosed passage of the nerve through the hyomandibular. The majority of ophidiiforms possess a condition corresponding to that in other euteleosts where the nerve travels a short distance within the anterior strut of the hyomandibular. The transmission of the nerve directly through a foramen in the anterior lamina of the bone is considered derived in *Acanthonus* and *Spectrunculus*.

The hyomandibular opercular process in *Acanthonus* is short (Fig. 7), in which respect it is like that of a wide spectrum of taxa including Carapidae, *Hypopleuron, Glyptophidium, Tauredophidium* and *Brotula* (Fig. 9B). Among other taxa, however, the process is long (*Neobythites, Sirembo, Monomitopus, Genypterus, Ophidion*) and is especially so in *Spectrunculus, Cataetyx* and *Bathyonus*.

Trigeminal nerve foramina and nerve courses

In *Acanthonus* the trigeminal, facial, optic and olfactory nerves exit the cranium through a common aperture. However, they pass through separate openings in a membranous septum which extends between the pterosphenoid-prootic and parasphenoid (Fig. 8). In having a common cranial nerve foramen *Acanthonus* differs from all other ophidiiforms examined (with the exception of *Bassozetus, Abyssobrotula* and *Lucifuga*); among those other taxa are major differences in the arrangement of the trigeminal-facialis foramina.

A narrow prootic lateral commissure is common to all the examined taxa with the exception of *Genypterus* and *Cataetyx*, both of which have a long lateral commissure (Fig. 10A). In all taxa the hyomandibular trunk foramen is narrowly separated from the trigeminal but the distance between the trigeminal foramen and opticolfactory aperture is variable. In *Genypterus* the distance is greatly increased due to elongation of the parasphenoid ascending process and pterosphenoid. In *Brotula* (Fig. 10C), *Spectrunculus* and *Cataetyx* the distance between the foramina is half that in *Genypterus* whereas in *Glyptophidium, Neobythites* (Fig. 10B), *Sirembo* and *Monomitopus* the separation is narrow. In *Lamprogrammus* it is intermediate between the first and second group of taxa. *Bassozetus, Abyssobrotula* and *Lucifuga* resemble *Acanthonus* in lacking a separate trigeminal foramen and in all these genera the common cranial nerve foramen is bordered by a lateral commissure. The size of the common cranial nerve foramen is variable but in *Brotula, Sirembo* and *Genypterus* it is narrow, exceptionally so in *Brotula* (foo, Fig. 10C) where an anteriorly directed laminar process rises from the midline of the parasphenoid and serves to separate the nerve tracts of either side (psp, Fig. 10C). According to Markle & Olney (1990) this process is a basisphenoid. However, in my specimen there is no suture to indicate that it is a separate element and the process stems from a medial ridge along the parasphenoid (pmr, Fig. 10C). In *Neobythites* the parasphenoid bears prominent paired ridges (pmr, Fig. 10B) but lacks a medial process. A basisphenoid does not occur in any ophidiiform or gadiform examined.

In *Acanthonus* the supraorbital trunk of the trigeminal nerve complex diverges from the infraorbital trunk at the point of emergence of the nerve bundle from the common cranial nerve foramen (Fig. 11). The RLA branch of the supraorbital (not shown in figure) extends dorsad entering a foramen between the sphenotic and pterosphenoid to pass caudad beneath the sphenotic and pterotic bones.

Among other ophidiids, bythitids and aphyonids examined

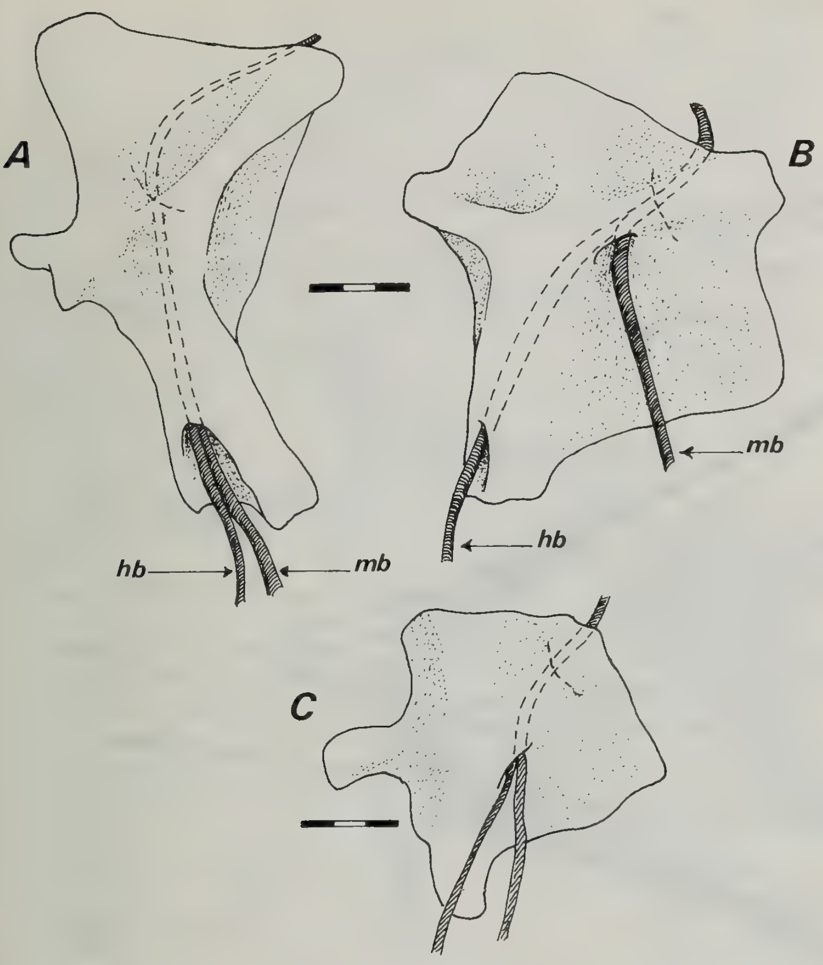

Fig. 9 Hyomandibular and its nerve courses in A, *Porichthys porosissimus*, B, *Brotula multibarbata*, C, *Neobythites gilli* (right lateral views).

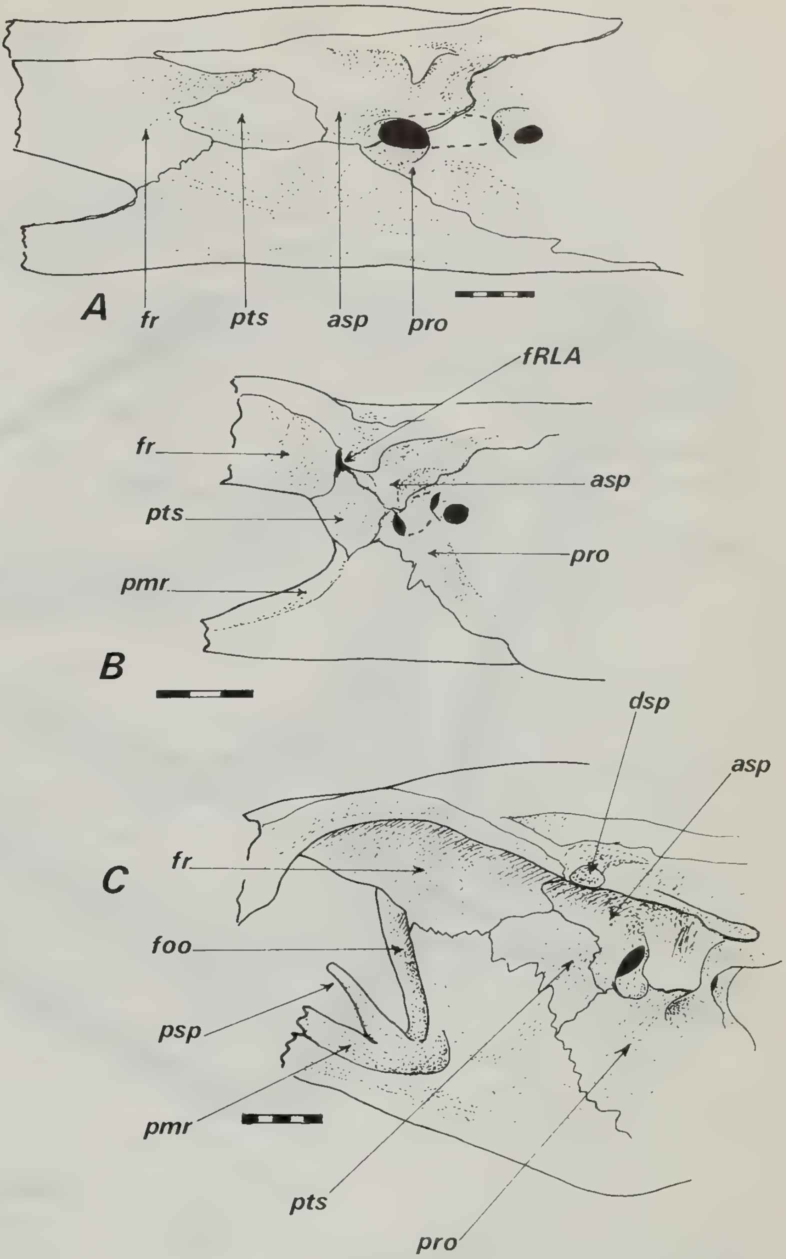

Fig. 10 Postorbital connections in A, *Genypterus blacodes*, B, *Neobythites steatiticus*, C, *Brotula multibarbata* (left lateral views). The extent of the trigeminal foramen covered by the lateral commissure of the prootic is indicated by dashed lines.

two groups of genera can be distinguished on the basis of whether the supraorbital trunk branches from the infraorbital trunk external or internal to the facialis chamber in the prootic. In *Brotula, Genypterus, Parophidium, Cherublemma, Ophidion* (Group A, Table 1) (Figs 12E & F), branching occurs within the chamber, the supraorbital nerves departing from the cranial cavity through separate foramina, as is the usual condition in teleosts (Fig. 12E). In *Dicrolene, Hoplobrotula, Sirembo* and *Neobythites* branching occurs at the point of emergence and the supraorbital nerves run dorsad along a channel in the outer surface of the sphenotic (Fig. 12A). In all other examined taxa (Group B, Table 1) branching occurs external to the chamber whether or not the exit foramen is common to the optic and olfactory nerves as in *Acanthonus, Bassozetus* (Fig. 12D), *Abyssobrotula* and *Lucifuga* or a separate trigeminal foramen as in the other above-cited genera (Fig. 12B, C & F).

Among gadoids and macrouroids the supraorbital nerves branch from the trigeminal trunk just prior to the latter's exit from the common optic-trigeminal foramen. The nerves then run medial to the pterosphenoid, departing from the cranial cavity *via* a foramen between the pterosphenoid and frontal to lie against the roof of the orbital cavity.

Branching of the supraorbital nerves external to the cranial cavity and lack of separate formina are considered derived conditions. The situation in *Hoplobrotula, Sirembo* and *Dicrolene* where marginal branching exists but a channel serves to conduct the supraorbital nerves dorsally is hypothesised to be a condition intermediate with the external branching and loss of trochlear and oculomotor foramina. The derivation of the derived state may be viewed as an anterior displacement of the nerve complex, possibly the result of temporal readjustments in the ontogeny of the brain and nerve trunks relative to the osteological development of the cranium (Fig. 12G).

Loss of the pars jugularis giving rise to a common optic-olfactory-trigeminal foramen is considered a synapomorphy for Gadiformes, linking Gadoidei with Macrouroidei (Howes, 1989; 1990; 1991). That a similar large-scale modification should also occur among ophidiiforms in what are apparently separate lineages questions the homologous *versus* homoplastic nature of the macrouroid and gadoid character.

Dorsocranial morphology

Gosline (1953) remarked on the nature of the parietals in ophidiiforms. Of the three taxa he examined, only in one, *Dinematichthys*, do the parietals meet in the midline. Cohen

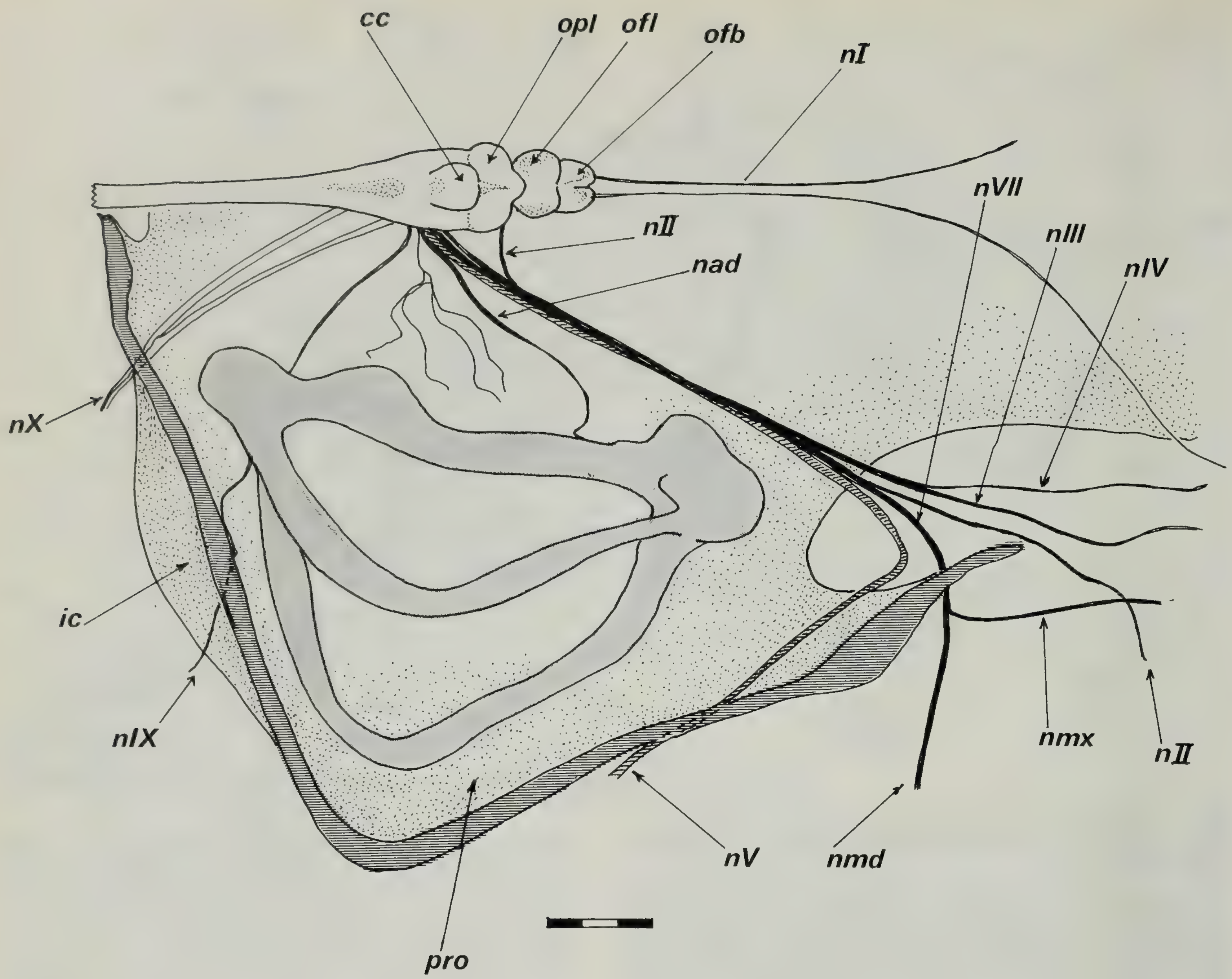

Fig. 11 *Acanthonus armatus*: brain and cranial nerves in dorsal view; the semicircular canals are shown in light shading.

(1974) shows that in *Brotulotaenia* the parietals almost meet anterior to the supraoccipital but are otherwise widely separated. In all the genera I have examined, the parietals are separated by the supraoccipital. In *Brotulotaenia* and in *Enchelybrotula* the parietals are extensive, being half the length of the frontals (Cohen, 1974; 1982) and although there is some variation in size in the genera examined, most do not exceed 25% of the frontal length. In *Acanthonus* the parietals are widely separated by the supraoccipital (the separation almost equals the width of the parietal; Fig. 13A); such wide separation occurs only in *Cataetyx* and *Bathyonus* (Figs 13C & 14A), taxa with broad and depressed crania.

There is considerable variability in frontal morphology among the taxa examined. *Acanthonus* differs from other genera in having the anterior border of the frontal laterally flared. In other taxa the frontal tapers anteriorly. The exception is *Glyptophidium* (Fig. 14E) where the frontal has a broadly rounded anterior margin and a straight lateral border. *Genypterus, Brotula* (Fig. 15B), *Sirembo* and *Spectrunculus* (Fig. 14B) have an extensive laterally open frontal canal. Anterior frontal crests, arising at the point where the bones meet the ethmoid bloc occur in *Lamprogrammus, Monomitopus, Neobythites, Sirembo* and *Glyptophidium*, the latter also having posterior crests at the junction of the frontal and supraoccipital (Fig. 14E). Frontal crests similar to those of *Glyptophidium* also occur in carapid ophidiforms (Fig. 21B of *Onuxodon* in Markle & Olney, 1990). A deep anterior medial cavity in the frontal midline, similar to the 'mucosal cavity' of gadoids occurs in *Monomitopus* and *Lamprogrammus* (Fig. 13B).

The autosphenotic of *Acanthonus* has a long, thick posteriorly curved lateral process (Fig. 13A). Of the taxa examined, only in *Spectrunculus* (Fig. 14B), *Monomitopus* (Fig. 14C) and *Brotula* (Fig. 15A) is the sphenotic process directed posteriorly but in these taxa it is small and spine-like. In other genera the process is either laterally or anteriorly directed. In *Genypterus* the sphenotic extends anteriorly to halfway beneath the length of the frontal (Fig. 15B).

The pterotic of *Acanthonus* has a prominently rounded posterior margin, a condition approached only by *Bathyonus* (Fig. 14A). In other genera examined the pterotic has a blunt or pointed posterior border.

Regan (1929) surmised that direct contact between frontal and parasphenoid diagnosed ophidioids (and blennioids); he had earlier (1912) illustrated this condition in *Brotula* where the frontal meets the anterior part of the parasphenoid

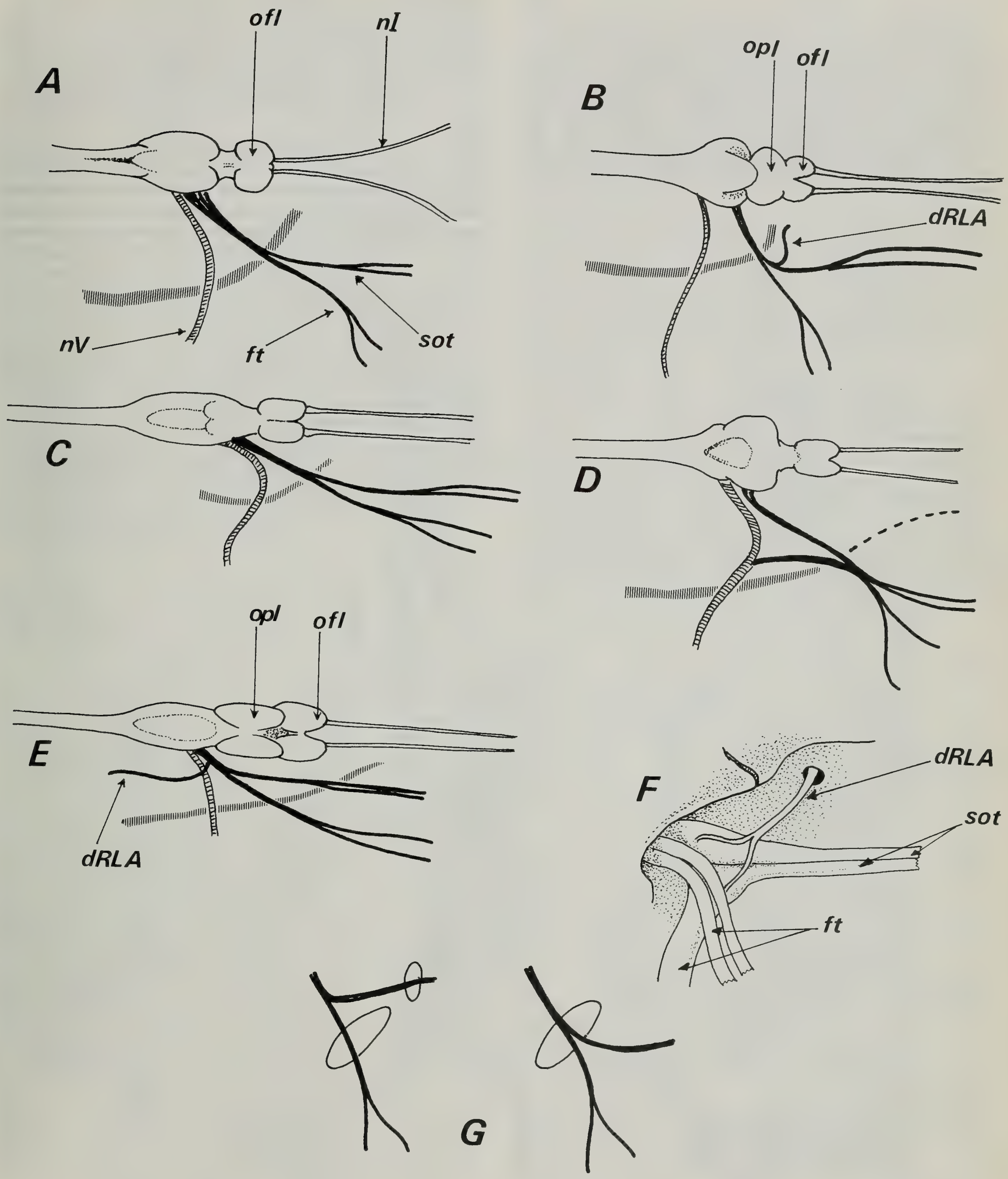

Fig. 12 Cranial nerve courses (semi-diagrammatic) in A, *Neobythites gilli*; B, *Lamprogrammus niger*, C, *Cataetyx* sp., D, *Bassozetus* sp., E, *Genypterus blacodes*, F, *Penopus* sp. Trigeminal branching external to the facialis foramen (ventrolateral view), G, Hypothesised shift of branching point of infraorbital and supraorbital nerves. Left, plesiomorphic ophidiiform condition (circular outlines represent foramina); right, derived condition with exit *via* single foramen and branching external to it. Shaded strips denote cranial wall.

ascending process. Gosline (1953) also recorded the condition in *Brotula* and *Dinematichthys*. Of the taxa I have examined, apart from *Brotula* (Fig. 10C), the feature occurs only in *Sirembo* and is thus certainly not diagnostic for ophidiiforms. However, among the Carapidae the frontal appears to contact the parasphenoid ascending process in nearly all the taxa illustrated by Markle & Olney (1990), the exception being *Encheliophis*. In view of the established monophyly of the Carapidae (Markle & Olney, 1990), the similar condition in the ophidiids (*Brotula, Sirembo*) and bythitid (*Dinematichthys*) appears to have arisen independently.

Olfactory nerve tracts

Gosline (1953) noted that the olfactory nerve pathway differed between *Brotula* and *Dinematichthys*. In the former the tracts are enclosed in a canal formed by the frontal and diverge from one another anteriorly, while in the latter, the tracts are free and diverge immediately from the olfactory lobes of the brain. In the taxa examined the variability is similar. In *Acanthonus* the tracts lie parallel for some distance before diverging (Fig. 11); the width of the cranial cavity allows a broad, unimpeded divergence of the tracts which lie medial to the sagittal interorbital membranous septa. This situation obtains in *Bassozetus, Lamprogrammus, Glyptophidium* and *Genypterus* (Figs 12B, D & E) but in other

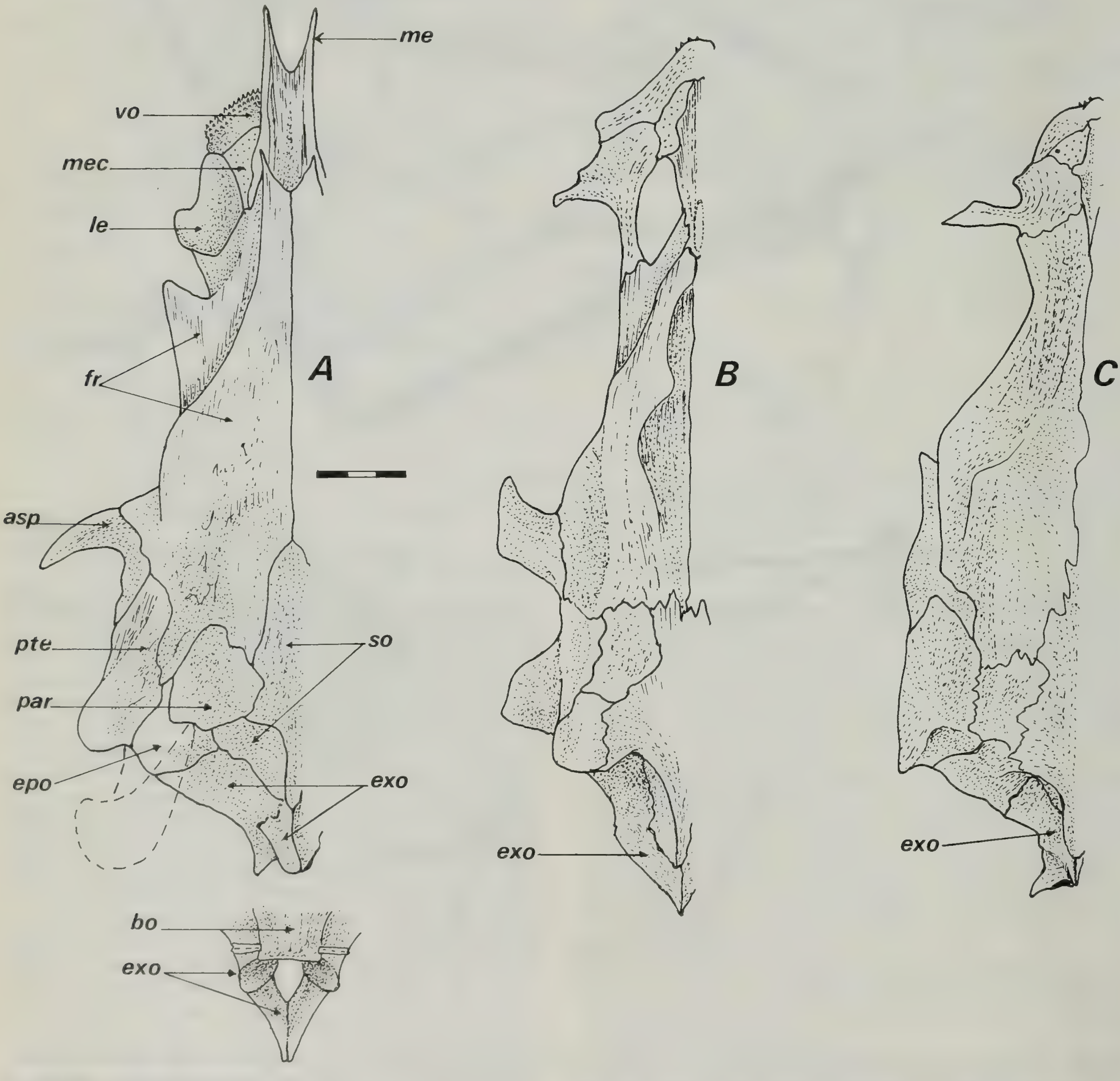

Fig. 13 Crania in dorsal views of A, *Acanthonus armatus*; B, *Lamprogrammus niger*; C, *Cataetyx sp*. In A, the posttemporal is indicated by dashed lines; below is a ventral view of the occipital condyles to show the extension of the exoccipital facets beyond the basioccipital facet.

genera the tracts are broadly divergent. In part these patterns are due to the distance between the forebrain and the olfactory organs which in *Brotula* is short, principally on account of the brain being particularly large and extending well forward. In *Monomitopus* a somewhat different situation occurs in that the forebrain enters the orbital cavity, the tracts running parallel for a short distance then diverging.

Position of glossopharyngeal foramen

Gosline (1953) referred to the varying position of the glossopharyngeal nerve foramen, apparently perforating the exoccipital in *Dinematichthys* and the intercalar in *Brotula*. Patterson & Rosen (1989) report that in all ophidiiforms they examined the foramen occurs in the intercalar. In *Acanthonus* an external examination of the cranium fails to locate the glossopharyngeal foramen. The fretted and honeycombed nature of the bone disguises any small foramina and its papery thinness is easily accidentally pierced giving rise to artificial 'foramina'. By following the route of the glossopharyngeal nerve within the cranial cavity it can be ascertained that the nerve exits from the posterodorsal border of the intercalar above the articulation of the lower limb of the posttemporal (Fig. 8). In other taxa examined for this feature the foramen is usually located in the centre of the intercalar either beneath or, more rarely, posterior to the site of attachment of the posttemporal limb.

Exoccipital, occipital condyles and first neural arch

Rosen & Patterson (1968: 425) noted that one of the features distinguishing gadiforms and ophidioids was the presence in the latter of a '. . . complex basioccipital joint with the first vertebra, involving the formation of a bony arch between the foramen magnum and the basioccipital facet'. Rosen (1985: 29) recognised that the batrachoid-lophiiform and ophidiiform-gadiform groups have the first neural arch and spine ankylosed with the first centrum and joined firmly to the cranium. Rosen (*op. cit.*: 50) in referring to gadiforms and ophidiiforms also noted that in some cases (specific examples were not cited) neural arches are incorporated into the exoccipitals and supraoccipital. Howes & Crimmen (1990) recognised such an incorporation in the neobythitine ophidiiform *Lamprogrammus* in which they identified both an incorporated neural spine and arch which formed the 'exoccipital' condyle and the first centrum which formed the 'basioccipital' condyle.

Although it is evident in all the ophidiiform taxa I have examined that there is a complete arch forming the rear of the cranium and bordering the posterior margin of the supraoccipital it appears that it is the occipital arch and not an incorporated neural arch. Evidence that it is the exoccipital is the presence of a suture with the entire length of the basioccipital and an unbroken suture with the supraoccipital. In many specimens the suture with the basioccipital is almost impossible to discern but the maceration of crania in both KOH and by boiling in water readily reveals the exoccipitals

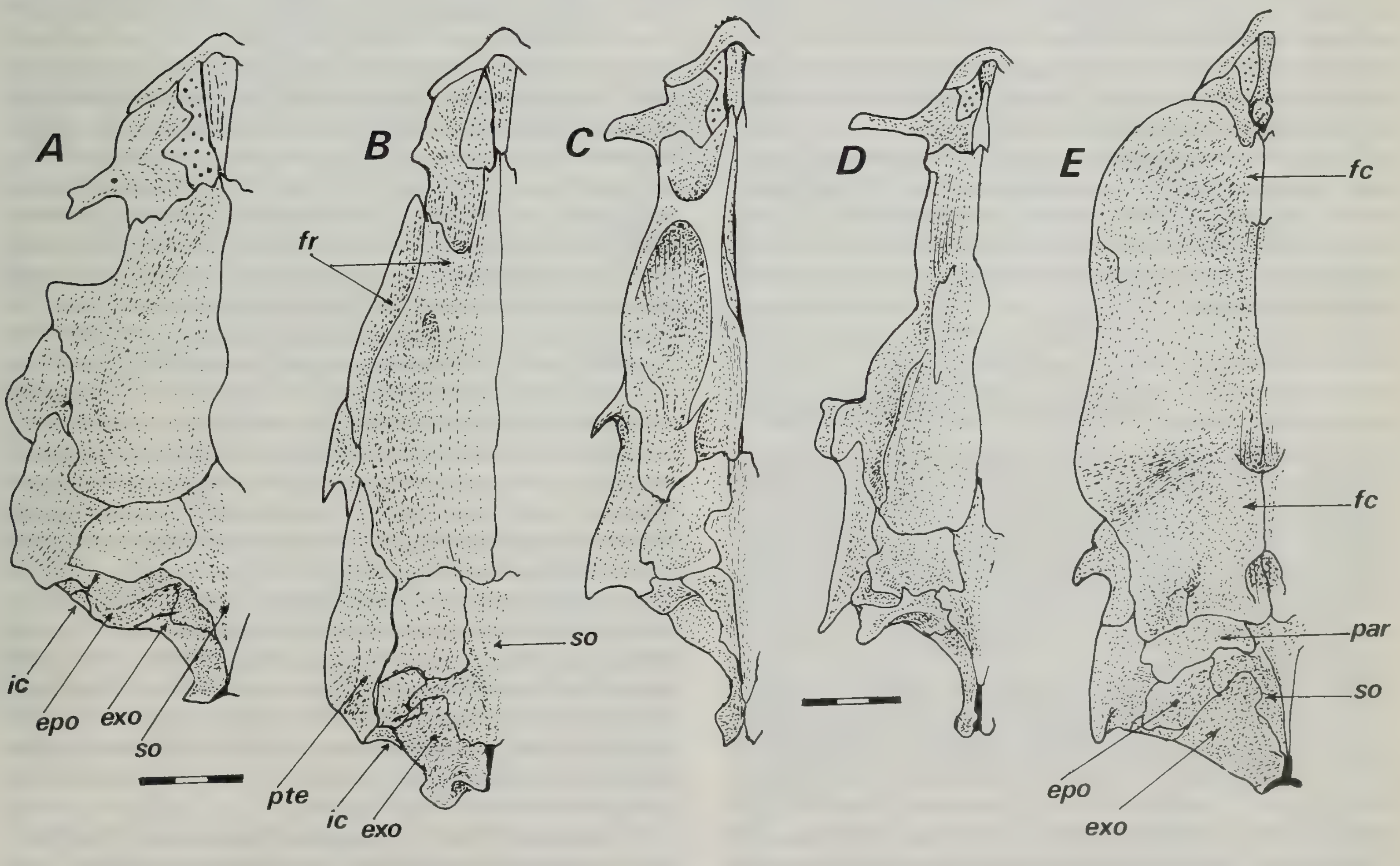

Fig. 14 Crania in dorsal views of A, *Bathyonus* sp.; B, *Spectrunculus grandis*; C, *Monomitopus metriostoma*; D, *Neobythites steatiticus*; E, *Glyptophidium macropus*.

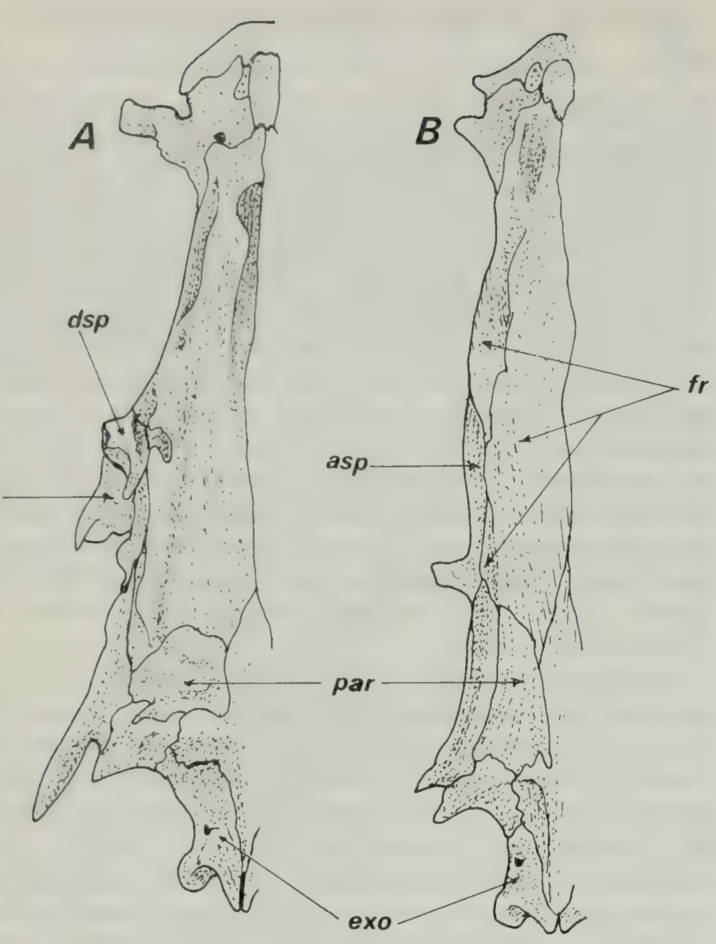

Fig. 15 Crania in dorsal views of A, *Brotula multibarbata*; B, *Genypterus blacodes*.

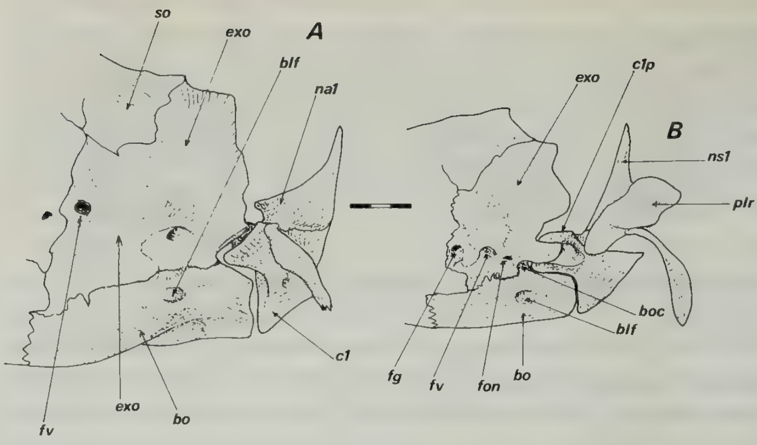

Fig. 16 Cranial-vertebral articulation in A, *Neobythites steatiticus* and B, *Ophidion rochei* (lateral views).

as single elements. Furthermore, in cleared and stained specimens cartilaginous laminae border the bones along the midline where they meet to form the floor of the foramen magnum. A foramen lying posterior to that of the vagus nerve transmits the occipital nerve trunk.

The posterodorsal extension of the exoccipital with consequent exclusion of the supraoccipital from the posterior cranial margin is a feature unique to ophidiiforms. In the Carapidae although the exoccipital is dorsally extended it does not rise high enough to occlude the posterior tip of the supraoccipital (Fig. 18C).

Rosen (1985: 50) noted that a possible synapomorphy between gadiforms and some ophidiiforms is the position of the exoccipital facets with respect to the basioccipital and the corresponding anterior extension of the prezygapophyses of the first centrum onto the occiput to meet the exoccipitals. Of the taxa examined here only in *Acanthonus* do the exoccipital condyles extend posteriorly beyond the basioccipital facet (Figs 13A, 18A), a feature otherwise peculiar to pediculate paracanthopterygians (cf. Rosen's 1985 fig. 35B and D). In all other taxa the posterior edge of the basioccipital facet lies in the same vertical plane or slightly beyond that of the exoccipital facets.

Rosen (1985) and Patterson & Rosen (1989) recognised two groups of ophidiiforms by their different occipital condyle morphology: Ophidiidae possess a plesiomorphic 'planar' arrangement of the exoccipital facets and Bythitoidei have derived 'cod-like', widely separated, tubular and cartilage-filled condyles. Rosen (1985, Fig. 36) illustrated *Ophidion* and *Ogilbia* as representing respectively the ophidiid and bythitoid conditions (Rosen's drawing of *Ogilbia* is reproduced here as Fig. 17B). Patterson & Rosen (1989) observed the planar condyle feature in *Brotula, Genypterus* and *Neobythites* as well as *Ophidion* but they did not list those taxa in which the supposed 'cod-like' articulation occurs. In the taxa examined here I do not find these marked differences (cf. Figs 17 with 16 and 18).

In *Ophidion* (Fig. 19D) the exoccipital facets are medially deep and are united to form a continuous articulatory surface; the lateral part of each facet is extended posteriorly into a 'condyle' and turned ventrad. The basioccipital facet is separated from the exoccipital by a deep forwardly directed cavity (boc). With two exceptions (see below) all other taxa (including the bythitoids *Ogilbia* and *Lucifuga*) have a 'planar' surface formed by medially united exoccipitals (Fig. 19A,B) although not as deep as in *Ophidion*; the lateral, condylar part of the exoccipital (exc) is variously angled and in *Glyptophidium* (Fig. 19F) faces directly ventrad. The basioccipital facet is separated from the exoccipital by a dorsally directed bursa-like cavity (boc) which accepts the ventral facet of the first centrum (clp, Figs 16B, 19D); see also Rosen & Patterson, 1968, fig. 10D of *Dinematichthys* and Howes & Crimmen, 1990, fig. 27 of *Lamprogrammus*. Apart from *Ophidion* the two exceptions to this condition are *Genypterus* (Fig. 19E) and *Acanthonus* (Fig. 19C), the only two taxa which have medially separated exocciptal facets. In *Genypterus* the separation is marginal but in *Acanthonus* it is extensive, and the facets appear as true 'cod-like' condyles. In *Acanthonus* the exoccipital facets extend beyond the basiocciopital facet (see above) and there is no davity between the basioccipital and overlying exoccipitals. *Genypterus* however, closely resembles *Ophidion* in having a horizontal cavity between the basioccipital and exoccipital facets into which inserts the anteriorly directed medial facet of the first centrum (Fig. 16B).

In ophidiiforms Baudelot's ligament is always confined to the basioccipital and is a consistent marker in separating the dorsal and ventral (which posteriorly become lateral and medial) sections of the epaxial muscle which inserts respectively on the anterior ribs and medial region of the swimbladder (see below). In *Acanthonus* Baudelot's ligament stems not from a fossa on the underside of the basioccipital but from the rim of the facet (Fig. 18A).

The first neural arch and spine display several modifications amongst ophidiiforms. In *Ophidion, Brotula* and *Genypterus* the bases of the neural arch are flattened anteriorly and expanded laterally which in *Ophidion* form wing-like

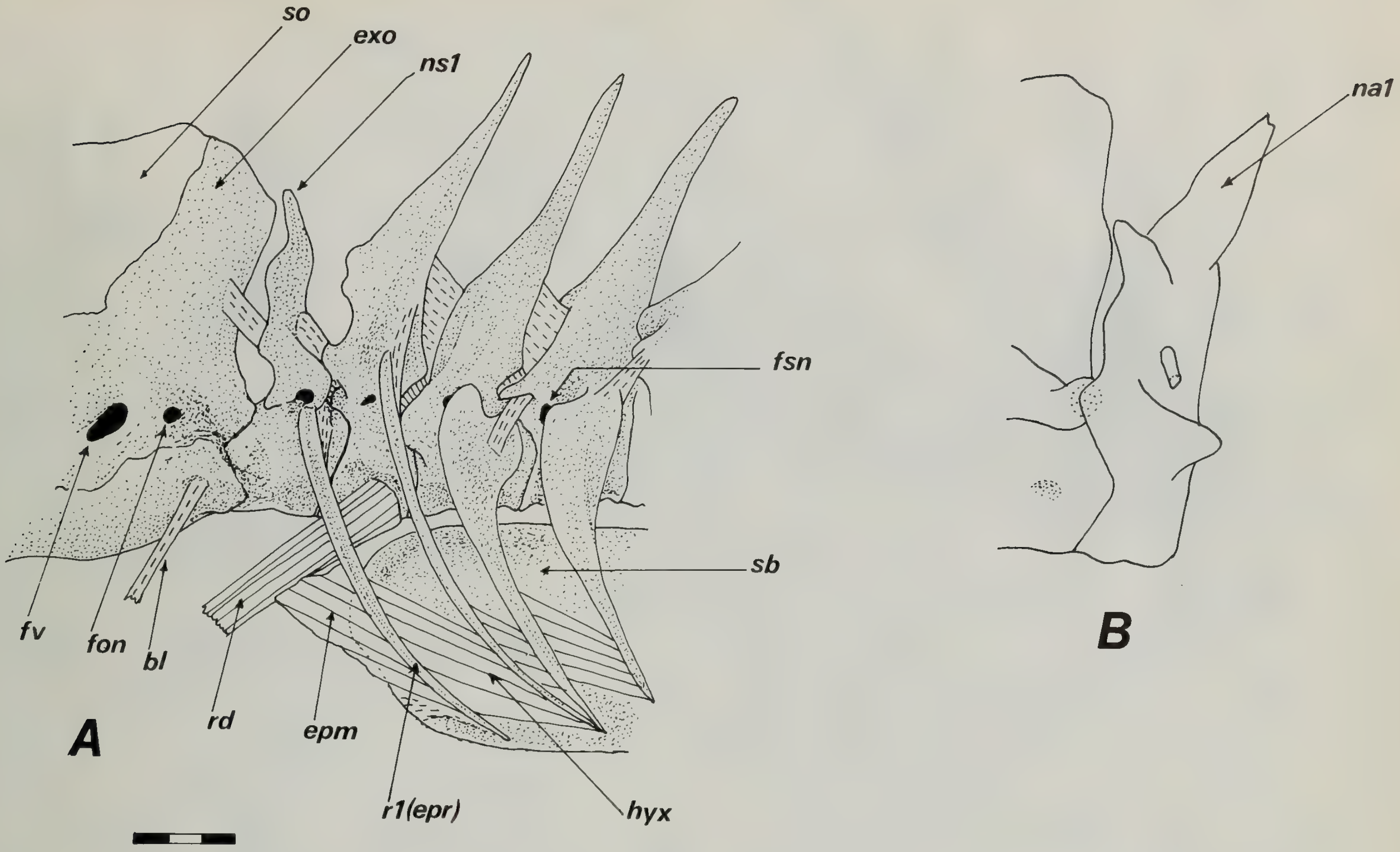

Fig. 17 Cranial-vertebral articulation (left, lateral views) in A, *Ogilbia cayorum*, also showing swimbladder connections (drawn from dissected and stained specimen); B, copy of Rosen's (1985) figure 36B showing the supposed designation of the first neural arch (guide-line absent in the original figure) and 'cod-like' condyles.

structures to which attaches a segment of epaxial muscle (Fig. 16B; Rose, 1961 and below). In some taxa (e.g. *Ogilbia*, and *Diplacanthopoma*, only the anterior base of the arch is autogenous with the centrum (Fig. 17A). In others including *Acanthonus, Bathyonus* and *Penopus*, (Figs 18A; 24B & C) the arch is reduced to a slender bone, the base of which is supported by only a narrow pedestal on the lateral ridge of the centrum. In other taxa (*Lucifuga* and *Spectrunculus*, Figs 23A; 25A) the neural spine has been lost, leaving the base of the neural arch autogenous and attached by post- and prezygapophyseal ligaments respectively to the succeeding neural arch base and the epioccipital.

It seems that among ophidiiforms and pediculates the skull has been posteriorly extended, in the former group by the dorsoposterior expansion of the exoccipital and in the latter by expansion and ankylosis of the first neural arch. Although there are similar modifications to the exoccipital-vertebral contact in pediculates and ophidiiforms the resemblances are not as close as recognised by Rosen (1985) and Patterson & Rosen (1989) so as to unite pediculates with bythitoids. As noted above, in almost all ophidiiforms the exoccipital articulatory facets form a continuous medial surface and the lateral margins retain a condylar form even though the articular surfaces may be variusly shaped and angled. In pediculates, however, there is no continuous exoccipital facet and the lateral 'condyles' are so modified as to have lost their condylar nature and in those taxa where they appear strut-like, their articular surfaces are sutured with those of the prezygapophyses of the first vertebra. There is no truly 'cod-like' cranial-vertebral articulation in any ophidiiform examined here and cartilage cores are present in all their exoccipitals. The most notable feature of the ophidiiform articulation is the presence in the majority of taxa of the angled bursa-like cavity lying between the exoccipitals and basioccipital and which occurs in all ophidiiforms and carapids (Fig. 18C). Markle & Olney (1990: 277) have drawn attention to this feature in referring to the medial ventral facet of the first centrum and it would seem that the modified basioccipital-vertebral articulation is a synapomorphy for ophidiiforms (including Carapidae).

Swimbladder and its connections

Acanthonus lacks a swimbladder, in which respect it appears to be derived (see below). The 28 genera examined for this feature display a plethora of conditions of swimbladder-vertebral column association. The variable nature of the association is revealed in muscle attachments, number and degree of hypertrophy of anterior ribs, their position on the vertebral column and features of the swimbladder itself. In addition the nature of the first free neural arch (discussed above) appears to be intimately connected with specific types of swimbladder-vertebral associations.

There are two basic types of swimbladder-vertebral connections:

(1) having the first (enlarged) rib attached to the first centrum and it and ribs 2 and 3 thickened with ribs 2 and 3 often expanded, extending horizontally and partially covering the anterodorsal surface of the swimbladder; the distal tips of all

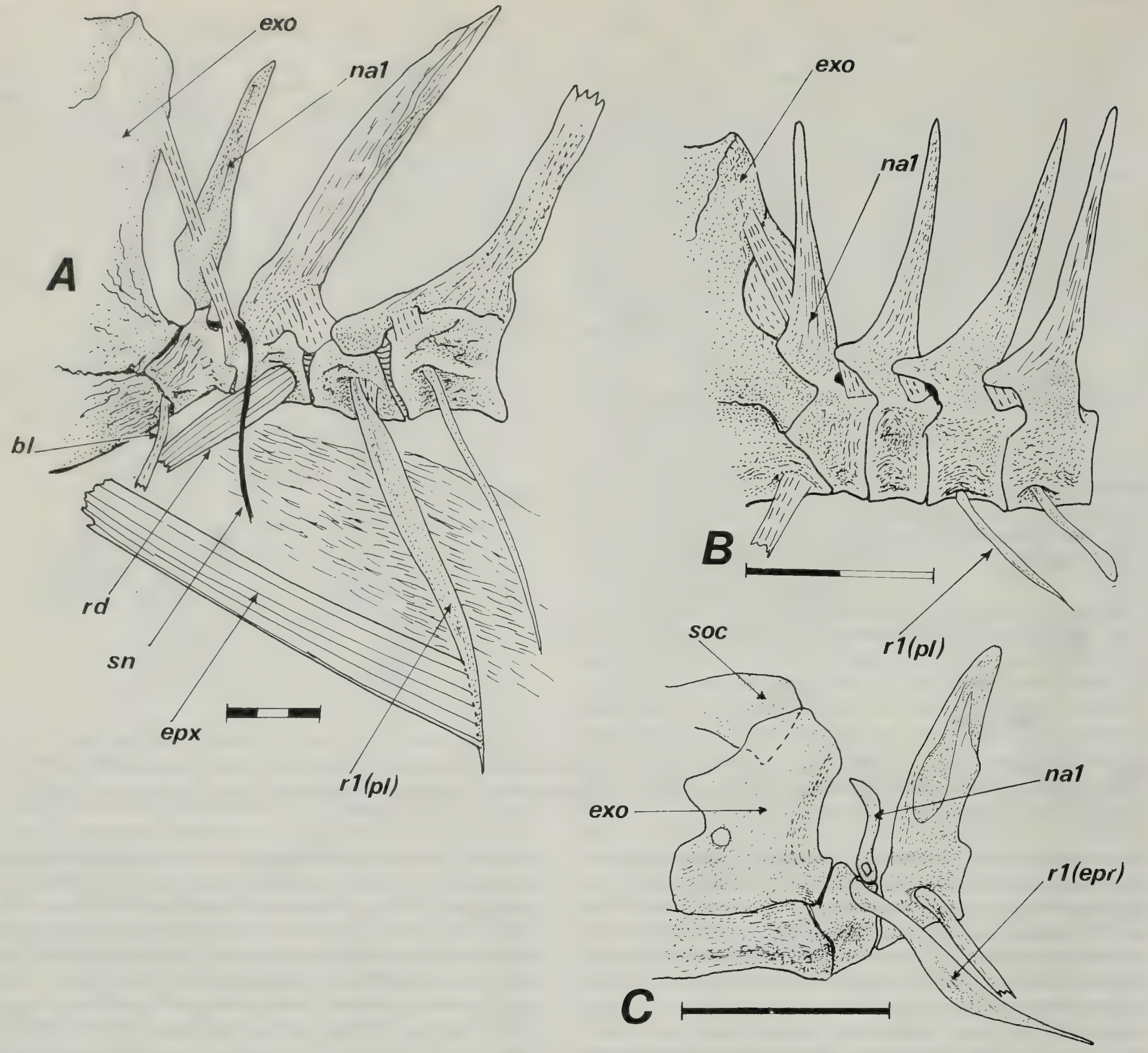

Fig. 18 Cranial vertebral articulation in A, *Acanthonus armatus*, also showing associated musculature (left, lateral view); B, *Barathronus bicolor*, membrane (hatched area covers space between exoccipital and first neural arch and spine; right side, lateral view; drawing reversed); C, *Carapus bermudensis*, (left, lateral view of cleared and stained specimen).

three ribs are attached to the swimbladder wall and well-developed muscles (lateral and medial) run between the cranium and first rib-swimbladder wall. The swimbladder is situated well forward, its anterior wall thickened by sclerification or ossification and sometimes the outer wall forms a flap or 'door' or separate elements (rocker bones) which are ligamentously attached to the ribs. A subgroup of taxa can be distinguished in which the first rib, although thickened is never expanded.

(2) having the first (large) rib attached to the second or third centrum, it and ribs 2 and 3 normal, vertical or somewhat posteriorly directed, all are free from the swimbladder. A narrow, outer band of epaxial muscle connects the first rib to the basicranium and a medial band runs to the dorsoanterior wall of the swimbladder. The swimbladder is situated far back, between the fifth and eighth centra and its anterior wall lacks any sclerification or thickening.

Some of the variation within these groupings is detailed below.

Group 1. Examined taxa with these features are Brotula, Cherublemma, Genypterus, Hypopleuron, Lepophidium, Ophidion, Parophidion

Rose (1961), Svetovidov (1961) and Courtenay (1971) have made detailed descriptions of the swimbladder and its cranial-vertebral connections in *Ophidion* (given as *Rissola* by Courtenay). These authors showed that sexual dimorphism is exhibited in the morphology of the swimbladder connections, the principal differences being the presence of an anteroventral element in males termed the 'rocker bone' by Rose (1961). The anterior pair of ribs are extended into wing-like structures which support the edges of the rocker bone (Fig. 16B). The expanded third rib forms a bony sheet

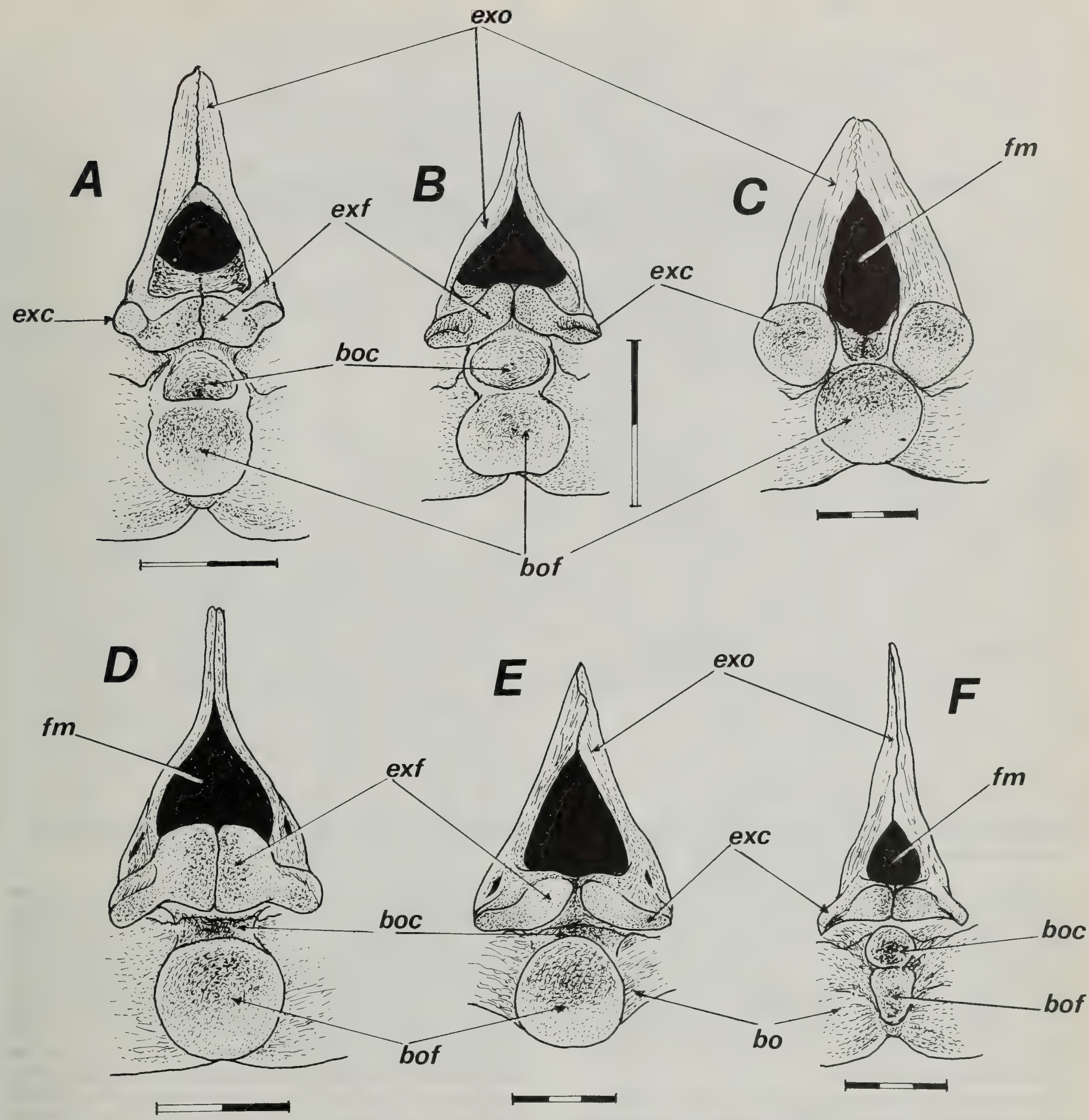

Fig. 19 Posterior views of occipital condyles of A, *Neobythites steatiticus*; B, *Ogilbia cayorum*; C, *Acanthonus armatus*; D, *Ophidion rochei*; E, *Genypterus blacodes*; F, *Glyptophidium macropus*.

covering the anterior region of the swimbladder. In these taxa the first neural arch is also modified (see above). Apart from *Ophidion, Brotula* is the only other examined genus to possess a rocker bone.

In *Cherublemma* (Fig. 20) the third and fourth-sixth ribs (possibly a combination of vertebral parapophysis and rib) are enlarged to form an ossified shield over the anterior part of the swimbladder; the anterior wall of the swimbladder (tunica externa) is almost completely excised, being attached by a ventral hinge and forming a 'trap-door' (sbc, Fig. 20) which is attached on either side of its upper rim to the tip of the first rib by a ligament (lcc, Fig. 20). When opened the door exposes a fenestra covered by the tunica interna (ti, Fig. 19B). The ribs of the third vertebra join together in the ventral midline to form a broad bony surface with paired depressions on which the dorsal lip of the 'door' closes. *Hyplopleuron* (Fig. 21) also has the first-third ribs expanded to the same degree; the tunica externa of the swimbladder is dorsally sclerified and laterally and ventrally the swimbladder is sequentially constricted, resembling the body of a caterpillar.

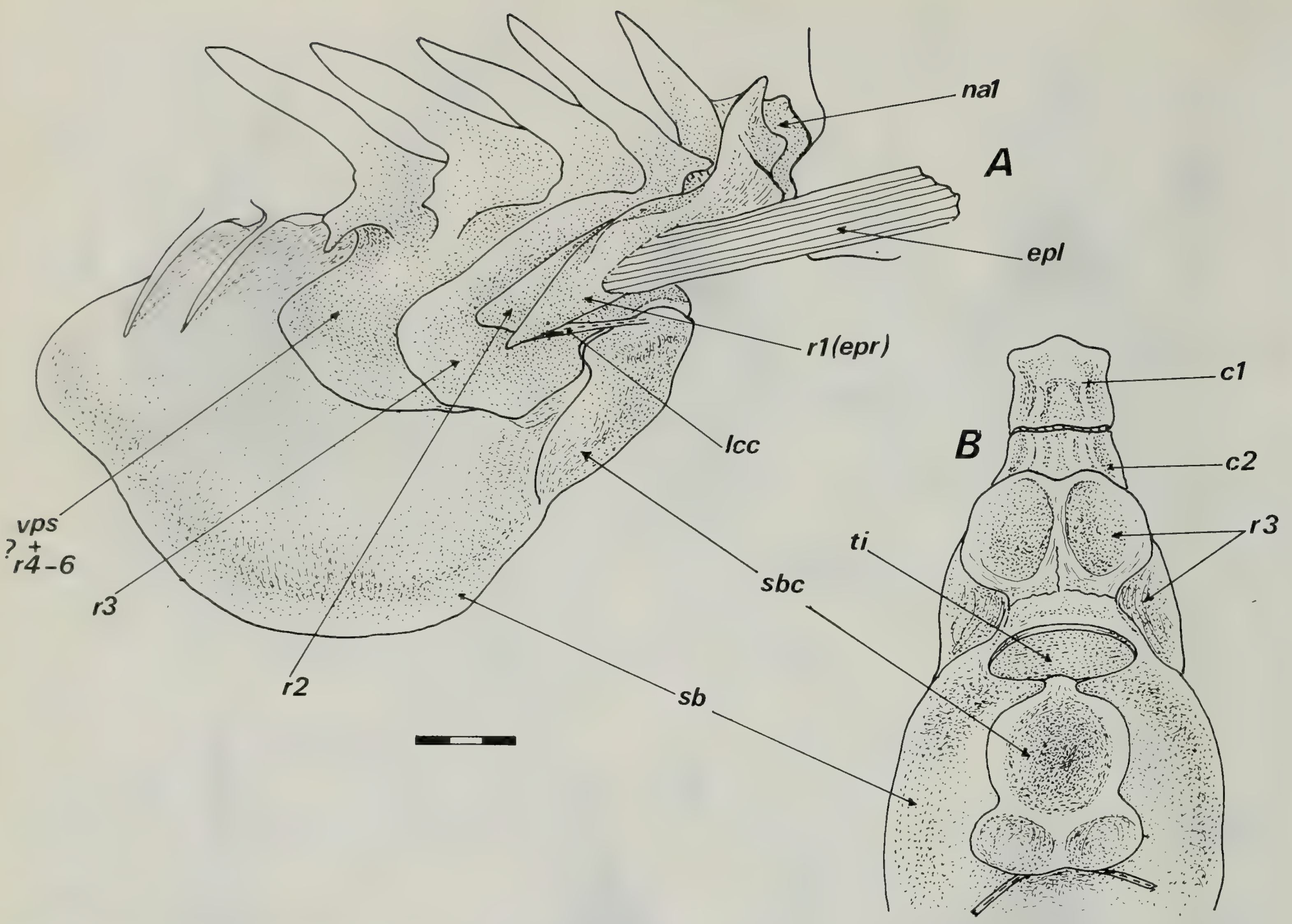

Fig. 20 *Cherublemma emmelas* (female). Anterior vertebral column and swimbladder in A, right lateral and B, ventral views. In B the cap of the swimbladder is shown reflected and with the ligaments cut away.

Owing to its expanded first rib and neural spine, *Lepophidium* (Fig. 22A) is also included in this group but there are several differences between it and the other included taxa. Ribs 2 and 3 are slender and rib 1 is attached to the head of the swimbladder by a thick, semi-ossified ligament which runs from the distal tip of the rib to bifurcate behind the second rib, the two branches (of normal ligamentous consistency) attaching to respective sites on the anterolateral and dorsal areas of the swimbladder wall.

Taxa recognised as forming a subgroup (see above) are: *Brosmophyciops, Dicrolene, Glyptophidium, Lamprogrammus, Monomitopus, Neobythites, Ogilbia, Pycnocraspedium, Petrotyx, Sirembo*.

In these genera the first-third ribs are stout but the first, unlike that of other Group 1 taxa, is not produced into a wing-like structure but resembles them in having the distal tips of the ribs ligamentously united and attached to the wall of the swimbladder (Fig. 22B). A separate muscle attaching to the medial part of the swimbladder occurs in some taxa (in *Brosmophyciops* it is particularly well-developed); the lateral band runs from the epi- and exoccipital regions of the cranium to join the compound swimbladder-rib ligament.

Lamprogrammus (Fig. 21) has a distinctly modified swimbladder and attachment. The expanded first-third ribs are entirely enclosed in silvery connective tissue which appears to be an extension of the compound ligament that invests the distal tips of the ribs in other Group 1 taxa; the nature of the tissue suggests that it might even incorporate the tunica externa of the swimbladder. The swimbladder itself is finger-like with a bulbous anterior cap, partially detached and hinged on its underside to the body of the bladder (sbc). When closed the dorsal rim of the cap is covered by a strong lip extending from the dorsal midline of the body of the swimbladder. A segment of the compound ligament attaches to either side of the cap. A paired muscle (epm, Fig. 21B,D) runs from the basicranium to insert directly on the swimbladder cap either side of the midline. The outer section of muscle (epl, Fig. 21B) runs to the proximal part of the first rib. A thick median ligament (lsv, Fig. 21B,C) stretches from between the ventrally directed parapophyses of the fifth centrum to the anterior lip of the swimbladder. The interior of the swimbladder is packed with dense, almost fibrous material.

In *Glyptophidium* the anterior ribs have a similar association with the swimbladder as in *Lamprogrammus* except that the swimbladder is more extensive and the tunica externa is firmly united to the underside of the centra by thick connective tissue. The swimbladder has a well-developed sclerified lip and is large and heart-shaped with a ventral opening exposing the tunica interna.

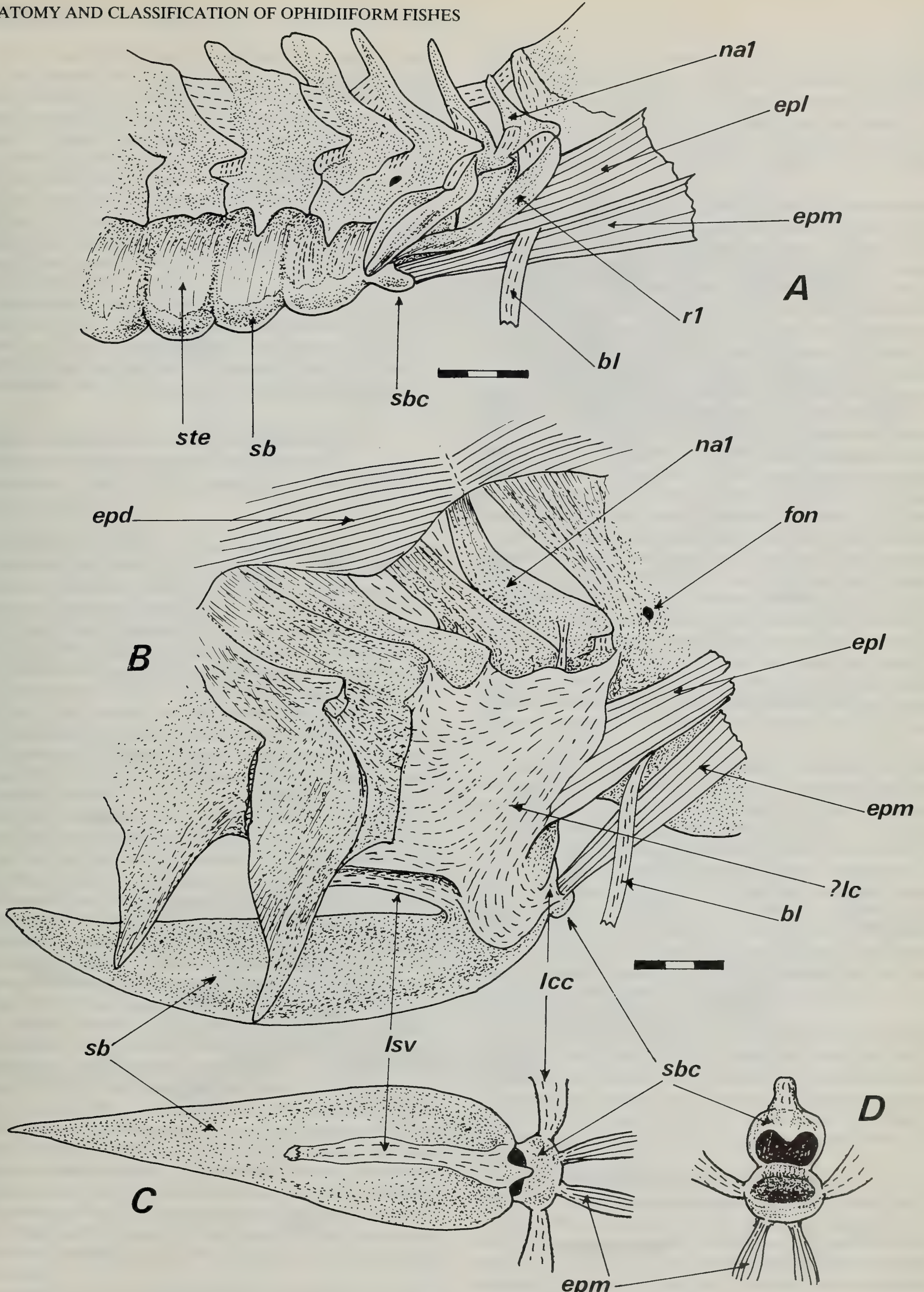
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Fig. 21 Swimbladder and its vertebral attachments in A, *Hypopleuron caninum* (male), right lateral view; B–D, *Lamprogrammus niger* (male), in B, right lateral view; C and D, dorsal and anterior views of swimbladder. In A, the ribs are shown as they appear upon superficial dissection, enswathed in ligamentous tissue; in D, the cap of the swimbladder is shown reflected.

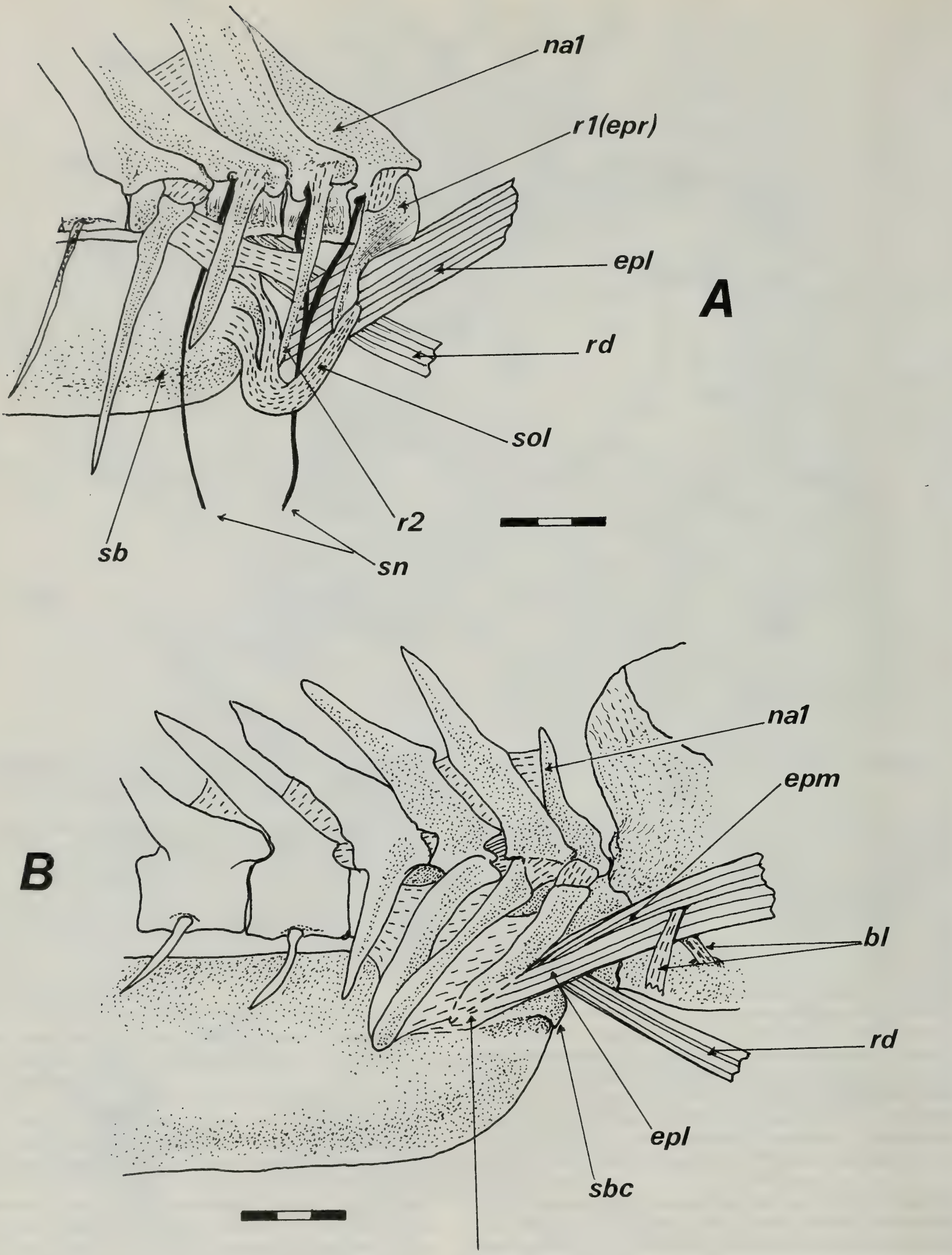
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Fig. 22 Swimbladder and its vertebral attachments in A, *Lepophidium cf. profundorum* (female); B, *Monomitopus metriostoma* (female), right lateral views.

Petrotyx and *Ogilbia* stand somewhat apart from the other taxa assigned to this group in having the swimbladder less directly connected to the anterior three ribs (Figs 17A, 22C). In *Ogilbia* (Fig. 17A) the first rib is scarcely thicker than the second although the third and fourth are proximally expanded. In *Petrotyx* (Fig. 23) all three anterior ribs have some expansion, the second only along its proximal part, and both the lateral and medial bands of epaxial muscle insert on the first rib although upper fibres of the medial band also insert on the second rib. The upper part of the outer (dorsal) muscle band passes over the first rib to become continuous with the lateral body epaxial muscle.

Luciobrotula possibly also belongs with this group. The second and third ribs are expanded and joined with the first to the all of the swimbladder by a compound ligament to which a lateral epaxial muscle attaches; there is no medial swimbladder muscle in the specimen examined (a female).

Group 2. Examined taxa with these features are: Abyssobrotula, Barathrodemus, Bathyonus, Bassozetus, Cataetyx, Diplacanthopoma, Penopus, Spectrunculus

Taxa of this group exhibit a broad spectrum of conditions but are united on the basis of lacking any great enlargement of the anterior three ribs and in having the first (longest) rib attached to the second or third centrum. The swimbladder is usually located in a posterior position and its anterior rim lies below the fifth-eighth vertebrae; it is elongate and extends to the 20–24th vertebrae. The muscles linking the swimbladder with the cranium have variable morphology; in *Penopus* (Fig. 24A) the muscle has its cranial attachment to the intercalar, pterotic and exoccipital and is divided by Baudelot's ligament, the outer segment attaching to the distal portion of the first rib, the medial segment extending caudad to insert on the dorsal surface of the swimbladder. The tips of the ribs are interlinked with hypaxial muscle but remain free of any direct connection with the swimbladder; in *Bathyonus* the tip of the 1st rib is attached to the postcleithrum (Fig. 24B). *Bathyonus* and *Bassozetus* have a similar arrangement except that in the former the medial muscle is attached to the swimbladder by a long thin tendon (Fig. 24B).

In female *Spectrunculus* (Fig. 25A) the medial segment of the muscle (it passes ventral to Baudelot's ligament) attaches not to the swimbladder but to the peritoneum to which the anterior wall of the swimbladder is itself connected. A pair of large, medial ventral projections, joined in the midline, extend from the fifth centrum in front of which the *retractores dorsales* take their origin. In the male (Fig. 25B) these medially united vertebral processes extend posteriorly in the form of a long deep strut to beneath the eighth or ninth centrum and the lateral epaxial muscle band inserts along the face of the strut. Separate, paired muscles run horizontally from the posterior border of the united vertebral processes above the strut inserting on either side of the dorsal midline of the swimbladder. This muscle is assumed to be a 'detached' part of that medial segment of the *epaxialis* which inserts on the vertebral ventral strut in the male and the peritoneum in the female.

In *Cataetyx* and *Diplacanthopoma* (Fig. 26) there is no separate medial muscle linking the swimbladder (both males and females examined), instead the lateral segment of the epaxial muscle inserts on a compound ligament with the distal tip of the first rib and the swimbladder wall. This situation is similar to that in taxa of the subgroup in Group 1 but differs in that the first rib of *Diplacanthopoma* and *Cataetyx* is curved anteriorly and a band of epaxial muscle distinct from the lateral myomeres runs diagonally backwards from the point of attachment of the first rib to the fourth or fifth rib (eps).

My observations on a single specimen of *Barathrodemus* sp. indicate that it belongs within this group of taxa but they also conflict somewhat with those of Carter & Musick (1985) on many specimens of *B. manatinus*. I do not find a separate pair of muscles connecting the fourth pair of ribs with the prootic; the only muscles in this position are the *retractores dorsales* which extend from the fourth centrum to the pharyngobranchials. Furthermore, in my specimen (a male) the medial muscles connecting the cranium with the swimbladder are separated from the lateral bundle by Baudelot's ligament (the usual condition; see above) and appear to stem from the exoccipital rather than the prootic. The muscles are tendinously joined to the anterodorsal surface of the swimbladder which lies below the eighth or ninth centrum and not the third as indicated in Carter & Musick's specimens. In most respects *Barathrodemus* most closely resembles *Penopus*. Although *Acanthonus* has no swimbladder, features of the vertebral column such as the slender anterior ribs, the first rib articulating with the third centrum and the first neural arch reduced and basally supported on a narrow pedestal (Fig. 18A) indicate its inclusion in this group. That *Acanthonus* has secondarily lost a swimbladder is suggested by the insertion of the lower (medial) segment of epaxial muscle to the first rib, rather than the upper (lateral) segment. Since it is the medial segment which inserts on the swimbladder, indications are that this segment has 'replaced' the original lateral connection.

Lucifuga (Fig. 23A,B) resembles taxa of Group 2 in having unexpanded ribs, however, the first rib associated with the swimbladder articulates with the base of the first centrum and the swimbladder is situated anteriorly as in Group 1 (Fig. 23A). The lateral muscle band attaches to the distal tip of the first rib and the swimbladder wall and there is no medial swimbladder muscle (in the male specimen examined), all features of the subgroup of Group 1 taxa. The lateral muscle band is, however, undivided by Baudelot's ligament which suggests that the lower and medial part of the muscle normally inserting on the swimbladder has been lost. Furthermore, Baudelot's ligament passes between two branches of the vagus nerve (Fig. 23A).

In the only aphyonid examined for these features, *Barathronus* (Fig. 18B), there is no swimbladder, the first pair of ribs articulating with the third centrum but having no muscular connections. According to Nielsen (1969) aphyonids lack ribs but the articulation with the ventral cavity of the 3rd centrum indicates that these processes are pleural ribs (see below).

Markle (1989) states that ophidiiforms typically have epipleural ribs on at least the first two centra and pleural ribs on all succeeding centra, citing *Porogadus* as exceptional in lacking epipleurals from the first two centra (Carter & Sulak, 1984). However, one group of ophidiiform, classified above as Group 2, consistently lack ribs from the first and often the second centrum and when ribs do occur they are short (e.g. *Spectrunculus*, Fig. 25A).

Markle (1989), Markle & Olney (1990) and Patterson & Rosen (1989) consider the anterior ribs to be epipleurals, a

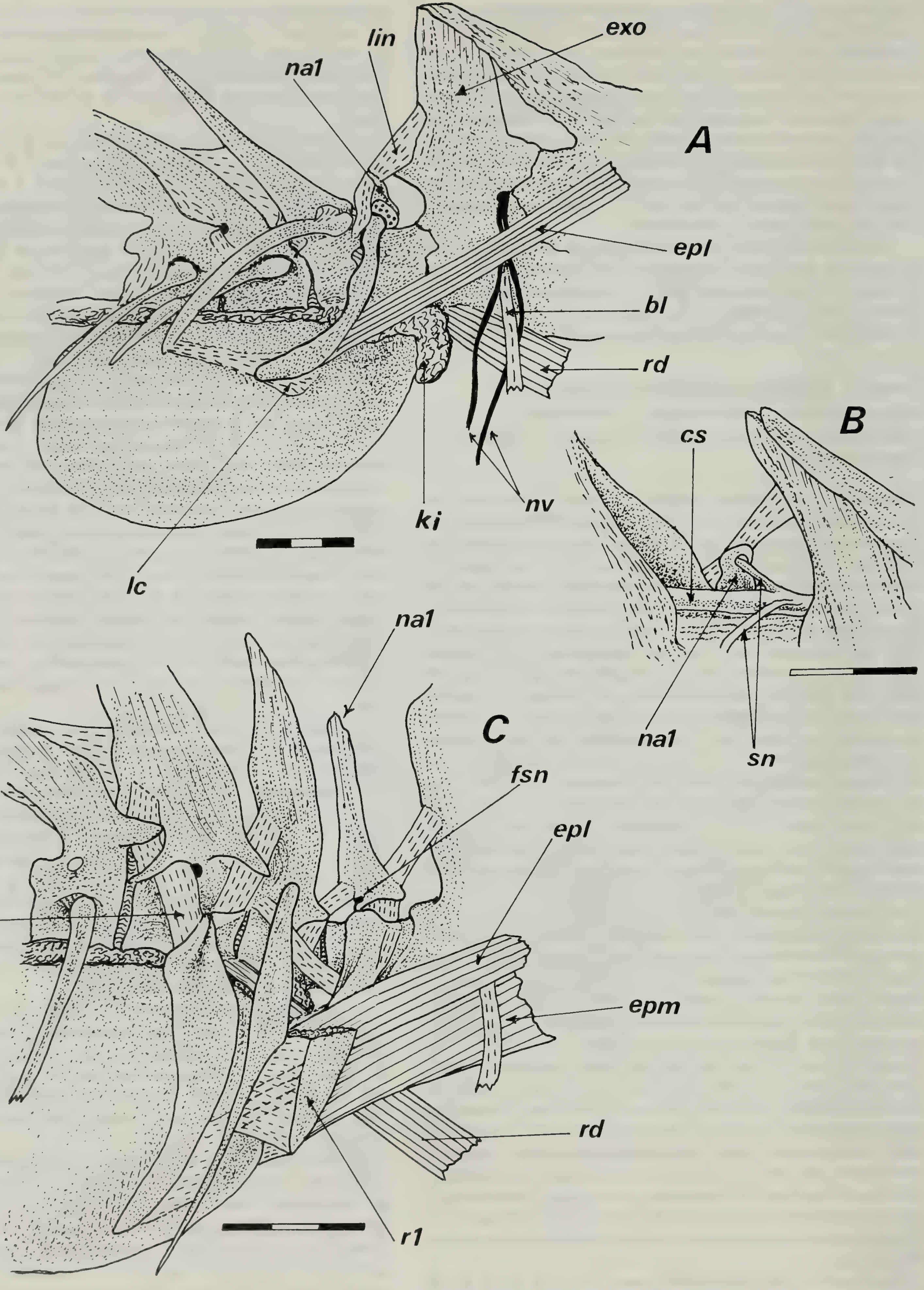
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Fig. 23 Swimbladder and its vertebral attachments in A, *Lucifuga dentata* (male), right lateral view; B, dorsolateral view of the first neural arch; the near-side has been removed to expose medial aspect of opposite half of the arch and the central spinal nerve and its associated branch; C, *Petrotyx sanguineus* (sex not determined), right lateral view.

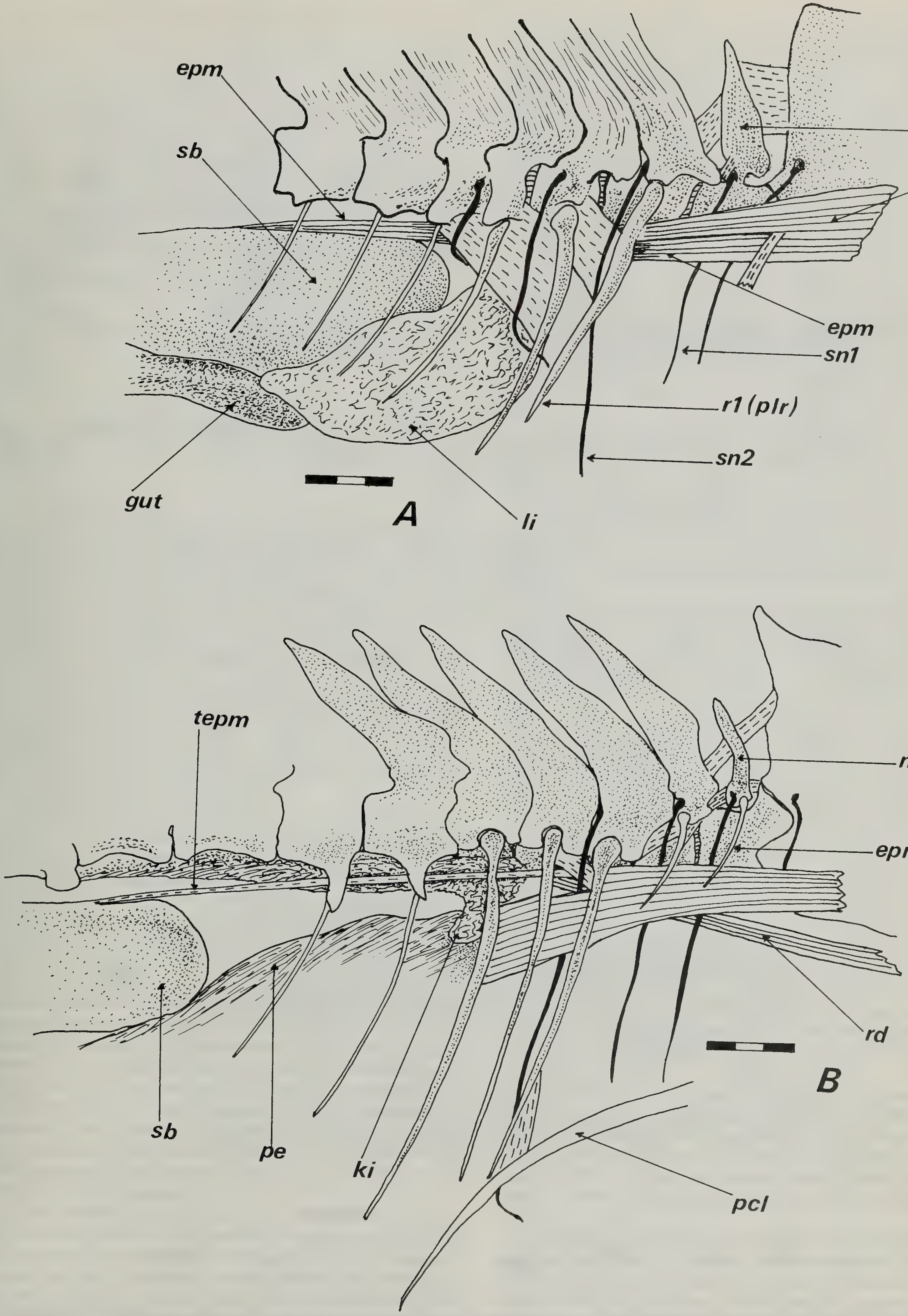
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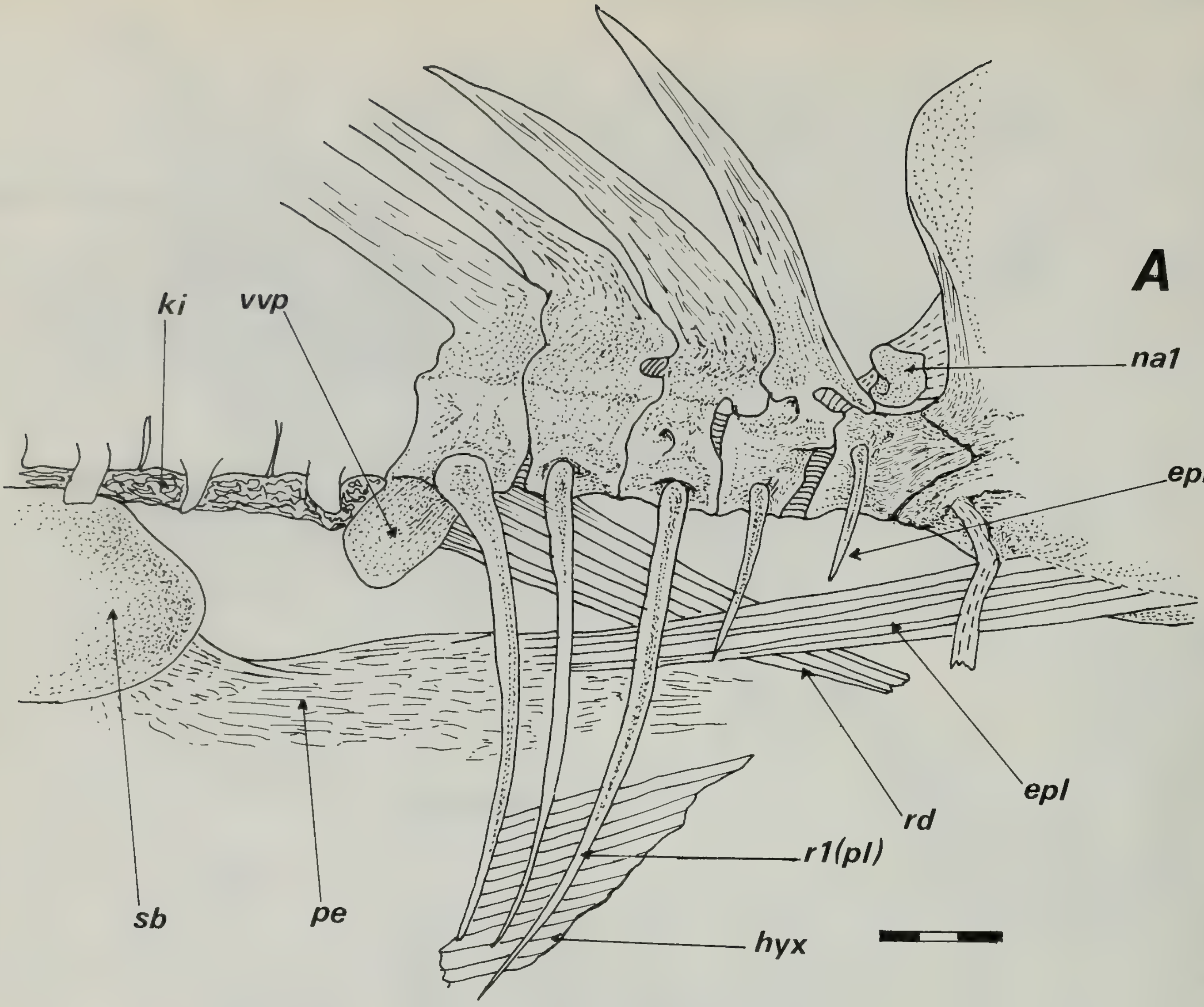
Fig. 24 Swimbladder and its vertebral attachments in A, *Penopus* sp. (male); B, *Bathyonus* sp. (female), right lateral views.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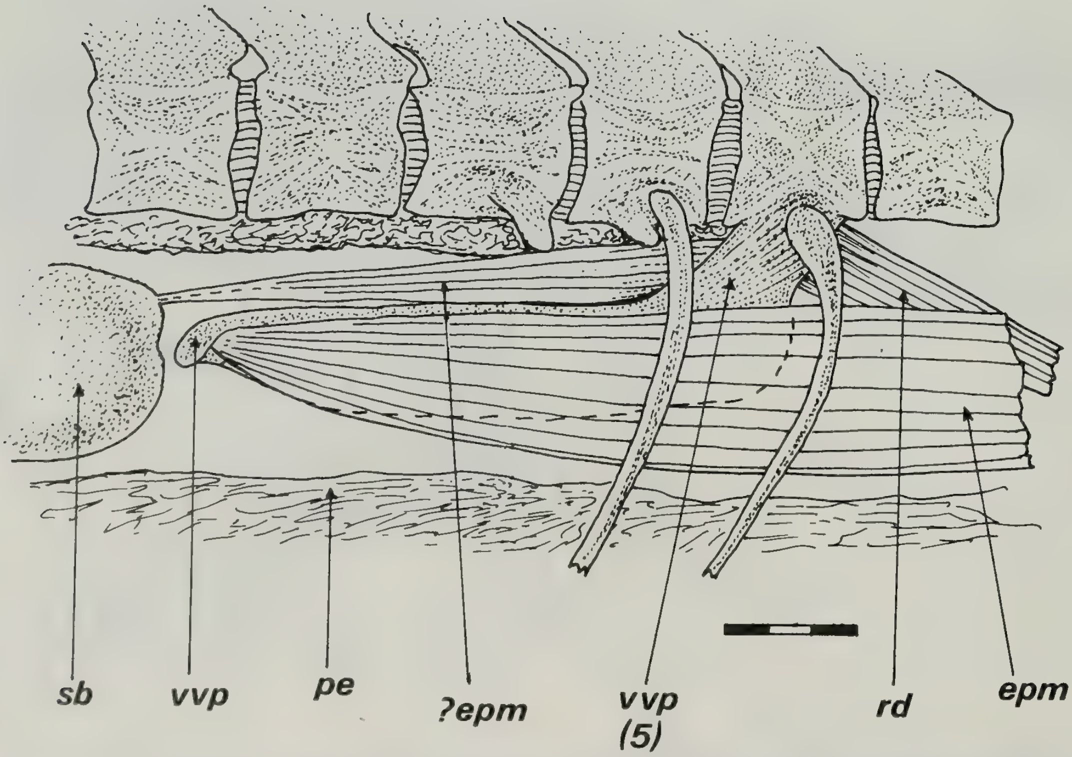
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Fig. 25 Swimbladder and vertebral attachments in *Spectrunculus grandis*. A, female; B, male, dashed line indicates margins of vertebral process, right side lateral views.

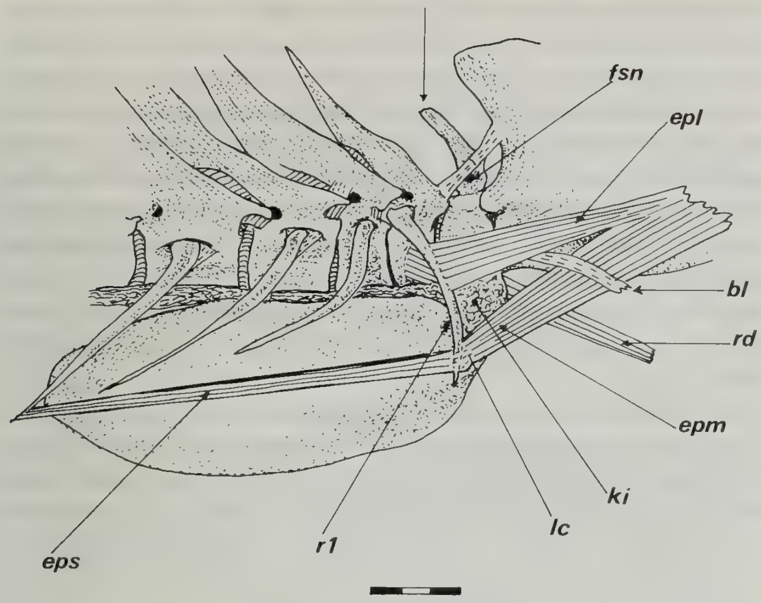

Fig. 26 Swimbladder and vertebral attachments in *Diplacanthopoma brachysoma* (sex not determined), right side lateral view.

view based principally on their topographical arrangement (see caption to fig. 8 in Patterson & Rosen, 1989). I would suggest that a further indication of their identity is given by the nature of their articulation, namely to the base of the neural spine (in *Ogilbia cayorum* the first epipleural articulates directly with the stem of the neural spine, Fig. 17A). In taxa of Group 2 all the ribs, apart from those on the anterior centra of *Spectrunculus* and *Bathyonus*, are pleural, that is they articulate with the ventral cavity of their respective centrum (Rosen, 1985: 50), none are expanded or directly associated with the swimbladder. Carter & Musick (1985) identify both a stout pleural and an epipleural rib associated with the first centrum in female *Barathrodemus* whereas in the male only an epipleural is present.

Markle & Olney (1990) state that ligaments connecting the epipleural ribs are absent in *Brotula* but present in the other ophidiids they examined; they also identify a compound swimbladder ligament uniting the tips of the anterior epipleurals as a synapomorphy for Carapini. I find interconnecting epipleural ligaments in all ophidiiforms examined, including *Brotula*, and a compound swimbladder ligament in those taxa assigned to the subgroup of Group 1.

To summarise the essential features of the swimbladder-vertebral column association: two assemblages of taxa can be recognised on the relationship of the swimbladder with the anterior (epipleural) ribs: those which have direct contact between the swimbladder and the thickened and expanded ribs (Group 1 above) and those where the swimbladder is isolated from the ribs which are nearly all pleural and never expanded (Group 2 above). Both assemblages contain taxa in which muscles connect the swimbladder with the cranium and in which sexual dimorphism is apparent in the presence/absence of medial muscles.

In the assemblage with expanded epipleurals there are modifications to the anterior wall of the swimbladder taking the form of sclerification and ossification (rocker bone and hinged openings). The same two assemblages can be recognised on the basis of the first neural arch morphology. In that assemblage with expanded ribs and modified swimbladder it is autogenous, usually thick and posteriorly inclined, whereas in the other assemblage the arch is usually separated into its two halves which are reduced in size joined ligamentously across the midline and connected to the centrum by a narrow bony or cartilaginous pedestal. It is assumed, based on the condition in other paracanthopterygians, that the expansion of epipleural ribs and their intimate contact with the swimbladder is a synapomorphy as are the various modifications to the anterior wall of the swimbladder. Similar features of the anterior vertebrae and swimbladder, including the development of a rocker bone, also occur in Carapidae (Courtenay & McKittrick, 1970; Markle & Olney, 1990). Markle *et al.* (1983) suggested that the paired sclerified structures of the swimbladder to which the anterior pleural ribs attach (Rose, 1961) may represent the precursor of the rocker bone. The presence of a semi-ossified ligament in *Lepophidium* (see above) which connects the swimbladder to the first epipleural rib suggests that such a structure could be implicated in the evolution of the bone. Markle & Olney (1990) dismiss the rocker bone and sclerification of the swimbladder in carapids as being synapomorphic with other ophidiiforms on the grounds that carapid monophyly is attested by a suite of six other synapomorphies, none of which occur in members of the wider group.

The modification of the first neural arch in both assemblages (expansion and thickening in one and reduction in the other) are seen as alternative derived states from the plesiomorphic slender, caudally sloped condition (Markle & Olney, 1990: 278).

Paired muscles having their connections with the swimbladder are common to both assemblages although a complex, medial division is absent from one subgroup (in Group 1 above) and some taxa of Group 2. The muscles identified here as lateral (dorsal) epaxial (epl) correspond to Rose's (1961) muscle M2 + M3 and Courtenay's (1971) 'dorsal sound producing muscle' and the medial (ventral) epaxial (epm) to Rose's (1961) muscle M1 (which in *Ophidion* and *Brotula* connects the rocker bone to the prootic) and Courtenay's (1971) 'ventral sound producing muscle'. Similar muscles in the Carapidae are named by Courtenay & McKittrick (1970) as respectively the secondary and primary sound producing muscles. The lateral (dorsal) band appears to be a segment of that part of the anterior epaxial muscle which has its attachment primitively to the posterior cranial roof and inserts on the first neural arch (see fig. 5 in Courtenay, 1971); the medial (ventral) segment likewise appears to be that part of the epaxialis which is primitively divided from the lateral part by Baudelot's ligament (see above), interconnects the ribs and its innervated by one of the occipital nerves. The presence of homologous muscles in Carapidae suggest they are primitive for Ophidiiformes *sensu* Cohen & Nielsen (1978).

The *retractores dorsales* muscles commonly originate from the third centrum in most ophidiiforms and Carapidae (Markle & Olney, 1990) but in taxa of one of the two assemblages recognised above as Group 2, the muscle originates from the fourth or fifth centrum (in *Spectrunculus* it runs from the anterior border of the united ventral vertebral processes, Fig. 25).

It is beyond the scope of this paper to attempt ascribing functional attributes to the various swimbladder arrangements described here. Suffice it to say that the swimbladder, anterior ribs and first free neural arch all appear to be elements of a single functional unit. Modifications to the first neural arch may have been signaled by the 'release' of the constraints imposed by the *epaxialis* due to its reorientation to the anterior ribs. The absence of a swimbladder is, judging by its widespread presence among ophidiiforms, a secondary loss which appears to have occurred independently in *Acanthonus, Typhlonus* and aphyonids.

It is noted that the two morphological groups recognised above correspond with ecological groupings. Group 1 are taxa which all inhabit shallow to mid-depths while Group 2 are taxa which are all deep to abyssal.

Cranial muscles

There are three features in which *Acanthonus* differs from other ophidiiforms: (1) almost the entire lateral face of the *levator arcus palatini* (LAP) is exposed, (2) muscle A1b is reduced to a narrow band originating lateral to LAP, (3) the *dilatator operculi* (do, Fig. 27) is extensive and exposed dorsally.

In all other taxa examined much of LAP is laterally covered by the adductor muscle (Ala and A2) but in *Acanthonus* only the lower border of the *levator* is covered by the adductor (Fig. 27). LAP is posteriorly divided and the hyomandibularis nerve runs through this division before bifurcating into mandibular and hyoid branches medial to the adductor; a separate, thin external branch of the mandibularis breaks through the muscle to innervate the tissue of the posterior part of the dentary. In other taxa the mandibularis externus is well-developed. Among the taxa examined, the size of *Acanthonus* LAP is equalled by *Xyelacyba* and *Tauredophidium* and exceeded only by that of *Spectrunculus* (Fig. 28).

In *Acanthonus* muscle A1b is shallow and thin, originating from the anterior border of the hyomandibular and overlapping the anteroventral tip of LAP. In other examined taxa muscle A1b is usually deep and thick, having a bifurcate

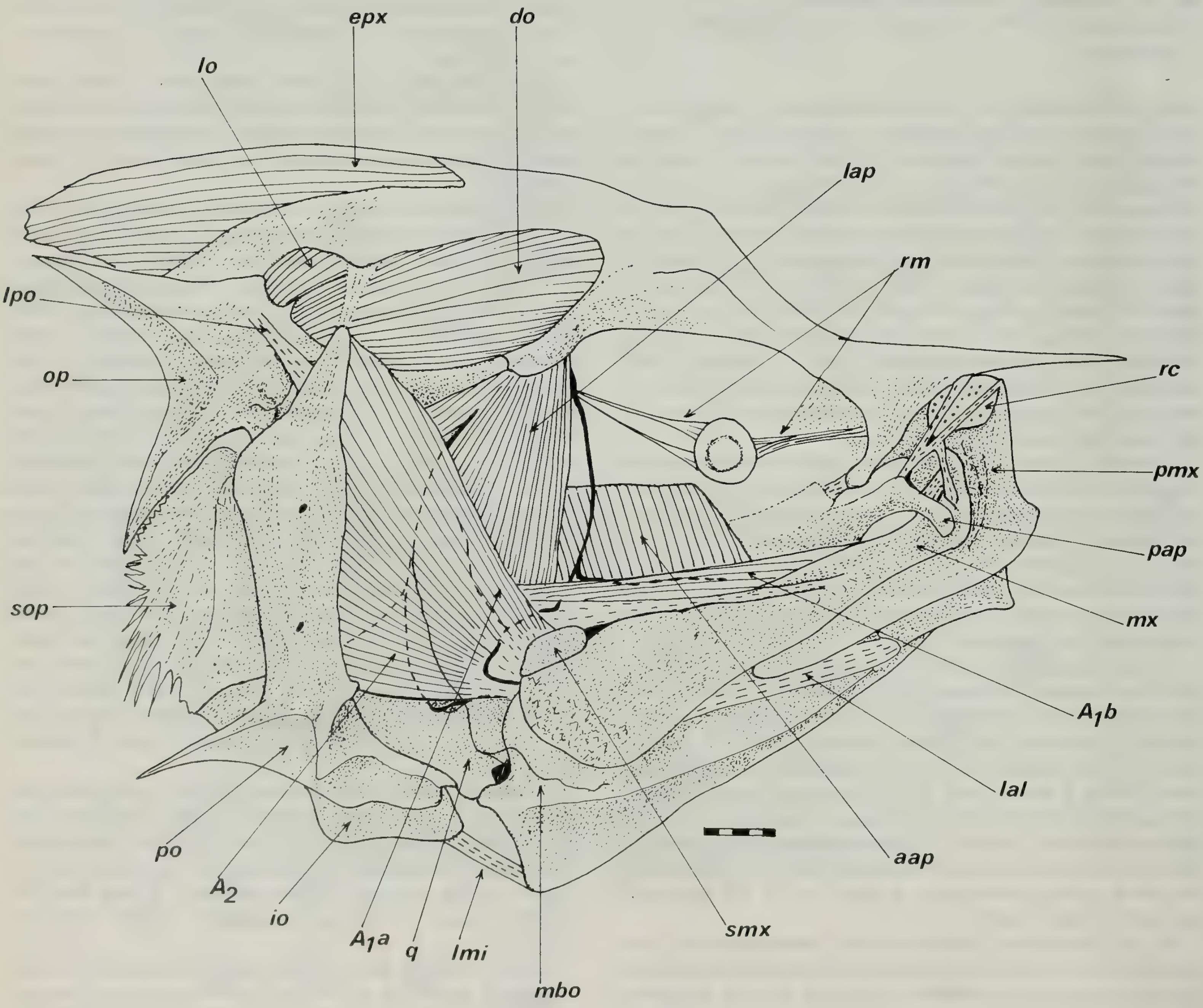

Fig. 27 *Acanthonus armatus*, right lateral view of head showing musculature; the operculum has been elevated to expose the suboperculum and so obscures the *adductor operculi* muscle. Nerves passing medial to muscles are indicated by dashed lines.

origin from either side of the LAP (Fig. 28). The medial segment stems from the metapterygoid or even the ectopterygoid and in *Bassozetus, Dicrolene* and *Spectrunculus* (Fig. 28B) joins the ventral edge of the *adductor arcus palatini*; in *Genypterus* some fibres of A1b even run from the palatine. The lateral portion always originates from the hyomandibular, which in some taxa (e.g. *Bassozetus, Lamprogrammus*; Howes, 1988, Fig. 25) may be the posterior border of the bone.

Muscle A1a was defined by Howes (1988) as that lying lateral to the ramus mandibularis of the trigeminal nerve even though that element might insert on the lower rather than the upper jaw (a more usual definition of A1a is that it inserts on the upper jaw). In ophidiiforms, Howes (1988) reported that the ramus mandibularis passes through the outer muscle bloc and so that section of the muscle lying lateral to the nerve is, by definition, A1a whereas that lying medial to it is A2; *Acanthonus* is no exception to this situation and the major

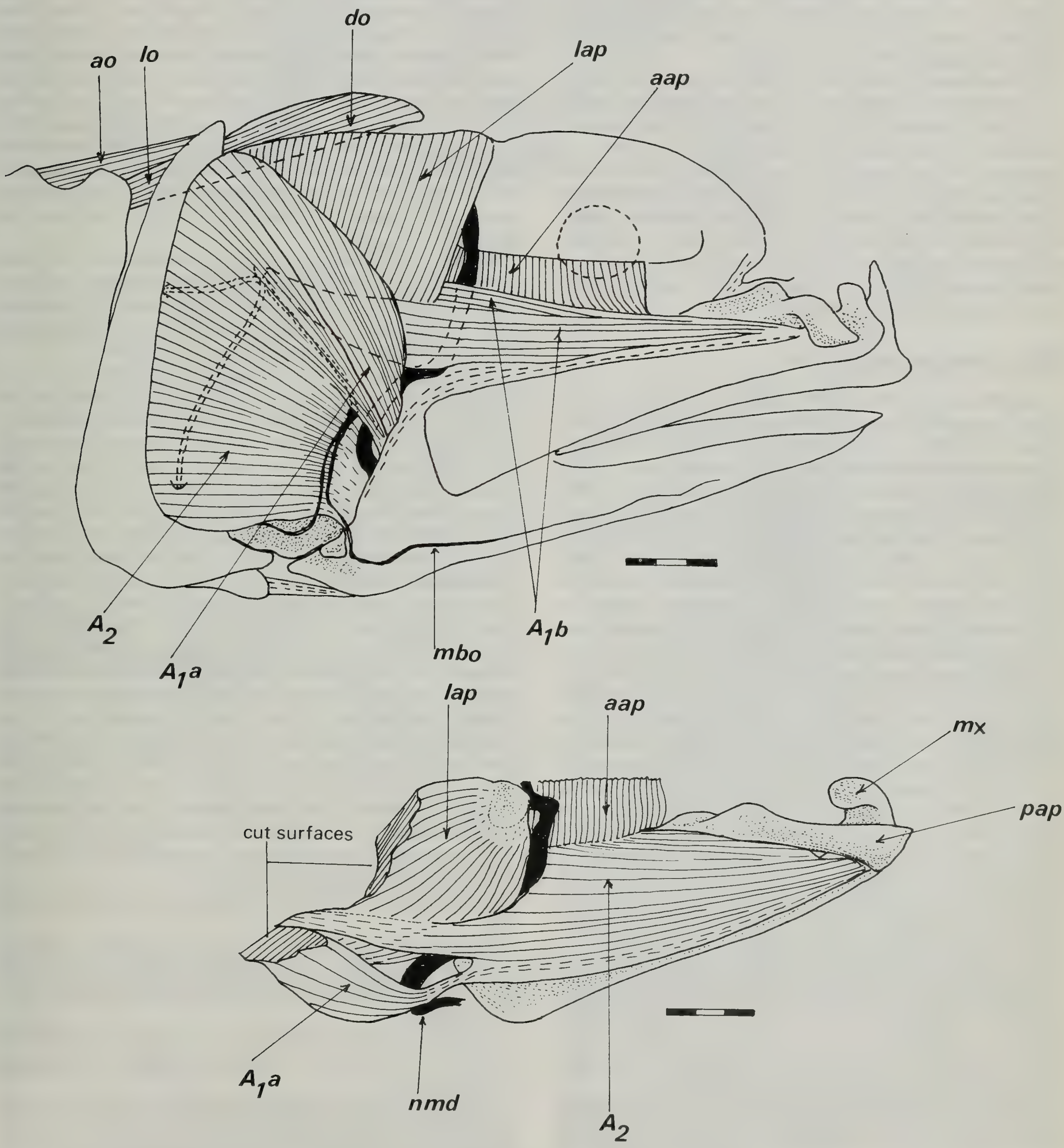

Fig. 28 Facial muscles and nerves of *Spectrunculus grandis*. Above, right lateral view; below, dorsal view of right muscle A1b showing its relationships with surrounding musculature. Nerves and medial extent of muscles indicated respectively by short and long dashed lines.

part of the adductor muscle which lies medial to the mandibularis nerve and inserts on the lower jaw is regarded as A2 (Fig. 27). As in gadiforms, muscle A1b lies lateral to the ramus mandibularis, or at least its outer division does; the divided 'A1b' of ophidiiforms appears to be synapomorphic for the group. A similar modificiation of 'A1b' is a diagnostic character of supragadoids (*sensu* Howes, 1991b) where 'A1b' lies entirely medial to A2 (Howes, 1988). *Acanthonus* displays a secondarily derived condition in having only an outer segment of A1b, the inner having been lost. The backward looping of the ramus mandibularis around muscle A1b in *Ophidion* (Howes, 1988: 35, Fig. 23A) sets this genus apart from other ophidiiforms examined.

In *Acanthonus* the *dilatator operculi* (do, Fig. 27) is extensive and occupies a cranial fossa in the pterotic and posterior part of the sphenotic. It is not covered by the *adductor mandibulae* or LAP muscles. In all other ophidiiform taxa examined, with the exception of two (see below) the DO runs behind the adductor and LAP muscles and originates from a narrow pterotic fossa situated on either the lateral or ventrolateral surface of the bone (Fig. 28, top). Only in *Tauredophidium* and *Xyelacyba* is the DO expanded and lies in a dorsally situated fossa and in the former the muscle is even more extensive than in *Acanthonus*.

Pelvic girdle and innervation

In ophidiiforms the pelvic girdle, when present, is reduced to a small triangular bone (in the Carapidae examined it is a slender rod with a cartilaginous anterior tip sandwiched between the tips of the horizontal cleithral limbs, making it in effect, a ventral appendage of the pectoral girdle (Fig. 29B). The anterior shift of the pelvic girdle has also involved modification of the muscles and nerves which motivate the pelvic fin rays. The *sternohyoideus* muscle, as in other teleosts, runs from the lower part of the cleithrum and inserts along the urohyal, but unlike the common situation, a ventromedial segment detaches completely or partially from the main body of the muscle, and its ventral attachment is to the cleithral symphysis above the pelvic bones (Fig. 29A). In most ophidiiforms the posterior border of the urohyal is near to the cleithral anterior margin and the medial segment of the *sternohyoideus* lies, for the most part, between the two outer segments. In *Acanthonus*, however, the urohyal is reduced in size and widely separated from the cleithrum and the medial segment of the *sternohyoideus* is well-separated from the lateral elements which extend further posteriorly along the cleithral limb (Fig. 29A). The pelvic muscles are restricted to the pelvic bone and lack any connection with the *sternohyoideus*. Hypaxial muscle runs forward between the cleithra and attaches to their medial walls; the *infracarinalis anterior* also extends forward to attach to each pelvic bone (Fig. 29C).

Other than *Acanthonus*, the distinct separation of the medial section of the *sternohyoideus* is present only in *Hoplobrotula, Sirembo* and *Dicrolene* (all members of the ophidiid subfamily Neobythitinae *sensu* Cohen & Nielsen, 1978) whereas in *Brotula* (Brotulinae) it is integrated to the same degree as in other neobythitines (i.e. *Bassozetus*).

The situation in *Genypterus, Lepophidium* and *Ophidion* (all members of the Ophidiinae *sensu* Cohen & Nielsen, 1978) is more complex than in other ophidioids. Cohen & Nielsen (1978) recognised the subfamily Ophidiinae principally on the possession of a modified cleithrum where the horizontal limb extends forward as a bony filament, thus advancing the pelvic girdle which is supported between the cleithral extensions. It should be noted that it is the medial bony laminae of the cleithra which extend forward and the cleithral tips remain in the approximate position of those of other ophidiiforms, *viz* beneath the basioccipital, but instead of meeting symphyseally they diverge and are connected in the midline only by hypaxial musculature. Although Cohen & Nielsen (1978) show the pelvic girdle sandwiched between the extended laminae, in the taxa examined here the cleithral bar attaches ligamentously to the pelvic bone (cle, Fig. 30). The *sternohyoideus* muscle is distally divided into lateral and medial portions. The majority of the posterior fibres of the lateral section attach to the urohyal while the ventral fibres converge into a tendon which attaches to the base of the urohyal; the medial portion runs directly to the inner face of the pelvic bones. The urohyal is extensive and canopy-like, forming a cover above the medial section of the *sternohyoideus* (ut, Fig. 30B); posteriorly the urohyal is firmly attached to the cleithral limbs by the *sternohyoideus*; anteriorly it attaches by a ligament to the 2nd hypohyal as well as to the ventrohyal (Fig. 30A).

Of the taxa examined, *Lamprogrammus* lacks a pelvic girdle and consequently any medial division of the *sternohyoideus* (Cohen & Rohr, 1992 detect the presence of a rudimentary pelvic girdle in *L. shcherbachevi*); the *supracarinalis anterior* attaches to the inner cleithral symphysis.

The innervation of the ophidiiform pelvic girdle has been described by Freihofer (1970) in *Brotula* and *Ogilbia* and by Machida (1988) for *Neobythites*. Both authors describe a hypertrophied branch of the ramus lateralis accessorius (RLA-PP) exiting from the posterodorsal region of the cranium and following a path along the posterior margin of the cleithrum which turns mesad and meets the third ventral spinal nerve (VSR3) to enter the two pelvic fin rays. In *Brotula, Hoplobrotula, Sirembo, Dicrolene, Bathyonus* and *Spectrunculus* the RLA-PP nerve crosses from the cleithrum to the pelvic bone *beneath* the hypaxial muscle, making it readily visible when the skin is removed (Fig. 30D). Each VSR3 descends to the ventral midline to run together between the *infracarinales anteriores* before meeting the RLA-PP. In the ophidiines *Ophidion, Genypterus, Parophidion* and *Lepophidium*, the nerve course is similar except that the RLA-PP and VSR3 pass together between the cleithral limbs and beneath the canopy-like urohyal (Fig. 30). In all other taxa examined (including *Ogilbia* and *Neobythites*) the RLA-PP is relatively thin, passes mesad to the cleithrum and hypaxial muscles and meets the vsr3 directly above the pelvic bone, both nerves exiting together between the *infracarinales anteriores* and entering the pelvic rays.

In summary, the respective conditions in the taxa examined are:

RLA-PP hypertrophied, running close to cleithral border and exposed laterally and ventrally, joining VSR3 posteriorly: *Brotula, Hoplobrotula, Sirembo, Dicrolene, Bathyonus, Spectrunculus*.

As above but RLA-PP and VSR3 running together through modified cleithrum and urohyal: *Ophidion, Genypterus, Lepophidium*.

RLA-PP thin, not exposed laterally or ventrally, joining VSR3 anteriorly: *Acanthonus, Abyssobrotula, Aphyonus, Barathronus, Bassozetus, Brosmophyciops, Cataetyx, Diplacanthopoma, Glyptophidium, Hypopleuron, Lamprogrammus, Lucifuga, Monomitopus, Neobythites, Ogilbia, Penopus, Porogadus*.

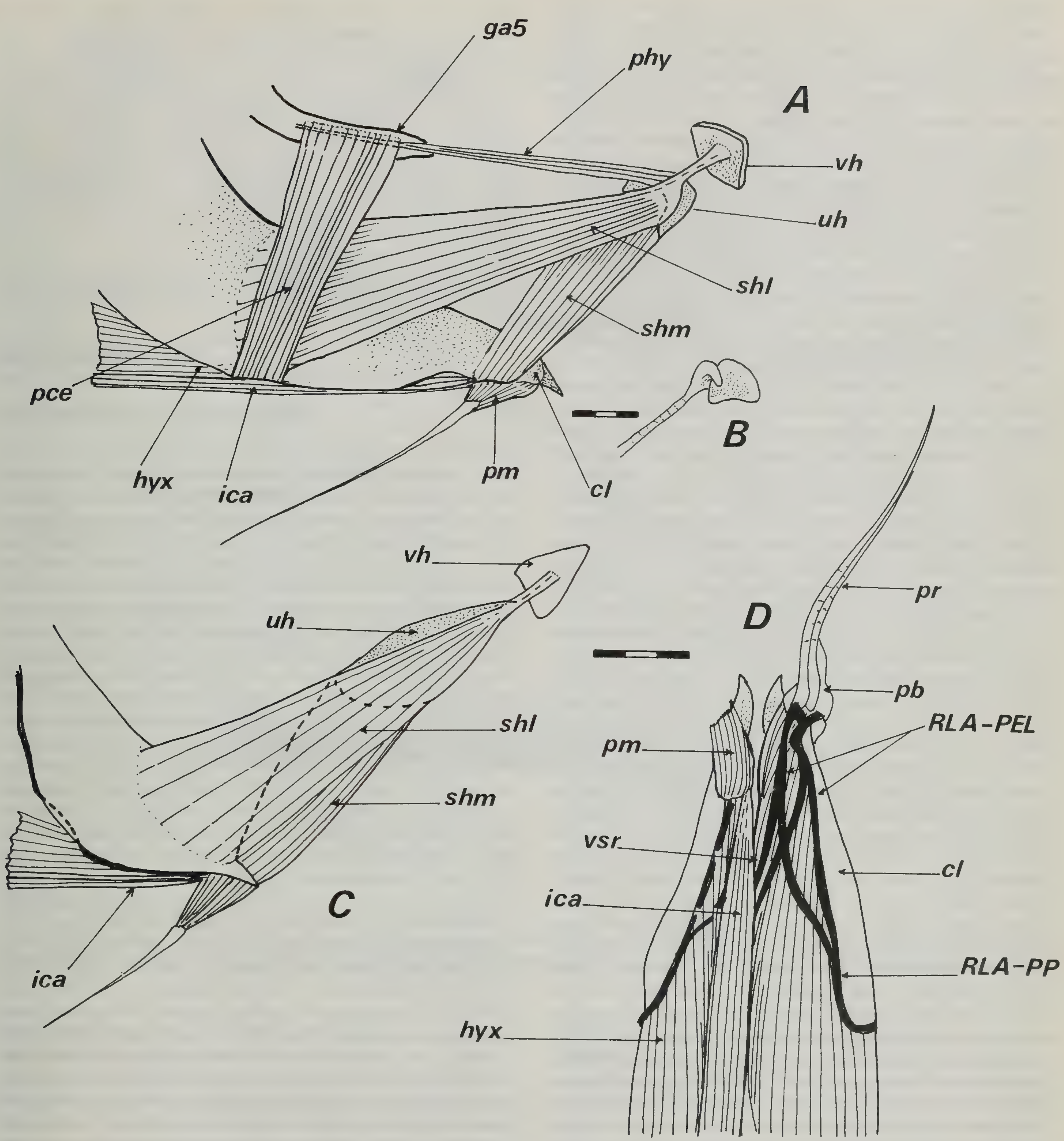

Fig. 29 Pectoral-pelvic girdle associations. A, *Acanthonus armatus*, right lateral view showing principal muscles. B, isolated pelvic bone with fin ray attached. C, *Bassozetus* sp., right lateral view of *sternohyoideus* muscle (dashed lines show limits of the medial part of the muscle and lower border of the urohyal). D, *Spectrunculus grandis*, ventral view; *infracarinalis anterior* removed from left side of fish to display nerves.

Pharyngohyoideus muscle

In all ophidiiforms and carapids examined the *pharyngohyoideus (rectus communis)* muscle extends from the urohyal to the fifth gill-arch (Fig. 29A). In the majority of taxa it runs from the anterodorsal tip of the urohyal and connects both elements with no intermediate attachment but in *Monomitopus* and *Neobythites* it also attaches to the third hypohyal and in *Spectrunculus* to the fourth. In the ophidiines *Ophidion, Genypterus* and *Lepophidium*, the *pharyngohyoideus* is a broad band-like muscle extending posteriorly from the face of the urohyal and attaching ligamentously to the fourth gill-arch as well as the fifth.

Howes (1988) noted that in gadoids and a few macrouroids *pharyngohyoideus (rectus communis)* attaches directly to the

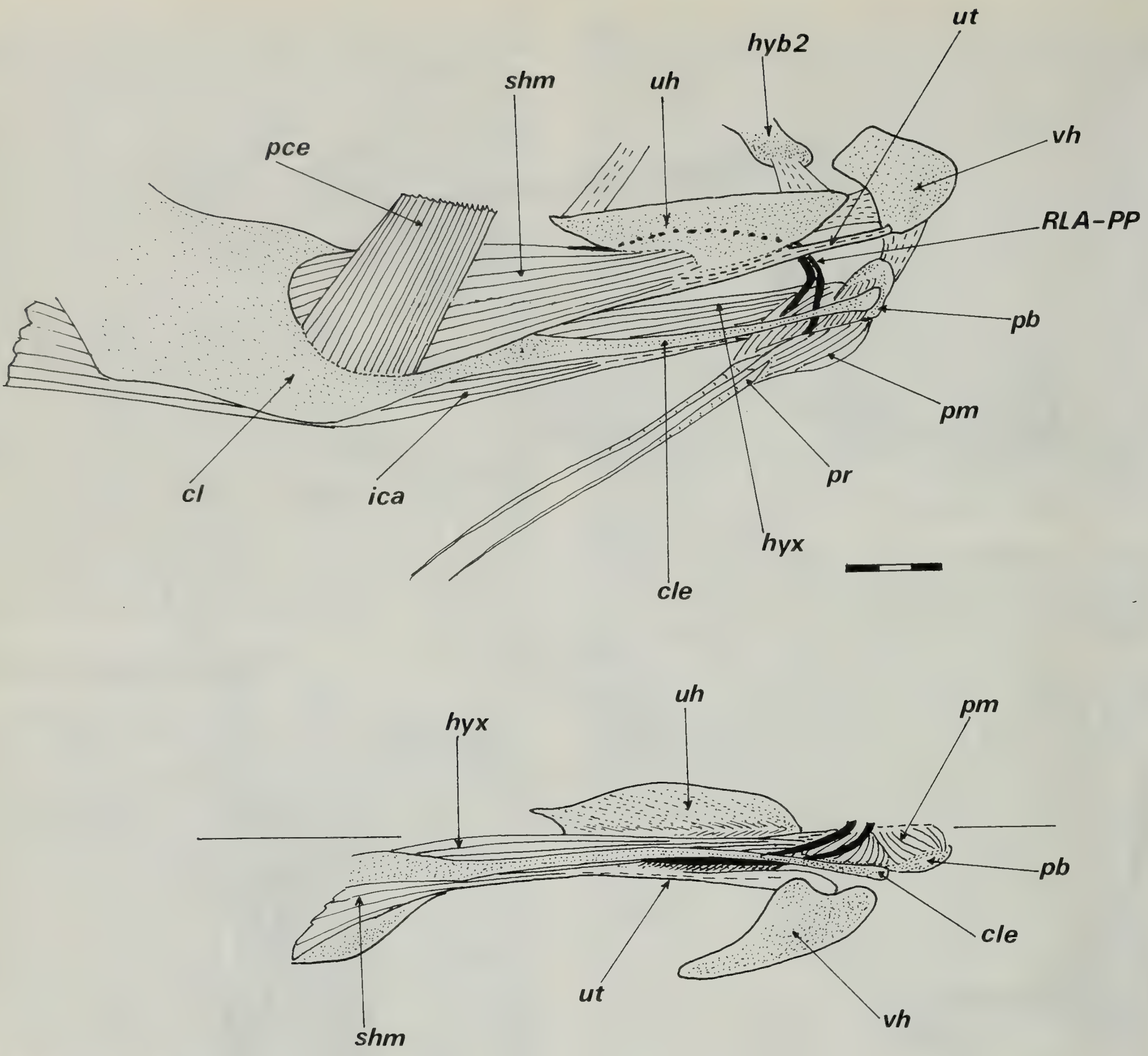

Fig. 30 *Genypterus blacodes*, pelvic girdle anatomy. Above, right lateral; below, ventral view. In the lateral view, the course of the RLA-PP nerve beneath the urohyal is indicated by a broken line. In the ventral view the muscles and nerves of the specimen's right side have been removed to expose the urohyal.

anterodorsal tip of the urohyal or *via* the *sternohyoideus* (as in ophidiiformes and carapids) whereas in most macrouroids it attaches to the bone's lateral face. The *sternohyoideus* mediated condition of the *pharyngohyoidus* in gadoids and some macrouroids was considered by Howes (1988) as having been derived from direct attachment to the urohyal keel, the (derived) acanthomorph state. In the group of ophidiform genera which possess the latter condition (ophidiines) there is no median keel, but merely a dorsal ridge so that the muscle inserts on the canopy-like base-plate of the bone (see above). Thus, the condition in ophidiines is considered to have been independently derived from that in other acanthomorphs.

Anterior mandibular pores

Acanthonus, in common with 50% of ophidiiform genera examined has a single opening in the dentary close to the symphysis which is the anterior opening of the mandibular sensory canal. In the other 50% of taxa there is an additional opening on the medial rim of the dentary, posterior to the ventral symphyseal opening. The medial aperture opens into the cleft where the isthmus (*protractor hyoideus* muscle) joins the dentary symphysis and is often covered by a fold of skin extending along the medial rim of the dentary (in *Dinematichthys* there are separate flaps of skin covering the medial openings). In *Spectrunculus, Monomitopus, Diplacanthopoma, Ogilbia, Dinematichthys* and *Lucifuga* the medial opening is large and in the latter three genera the dentary rim is notched at the medial opening (med, Fig. 31A). In *Sirembo, Hoplobrotula, Ophidion, Lepophidium* and *Genypterus* the medial opening is small and narrowly separated in the midline from its antimere (Fig. 31B) but in *Porogadus* and *Tauredophidium* the medial openings are extensive and widely separated. In *Brotula* the so-called barbels are tubular extensions of the medial openings which communicate directly with the mandibular canal.

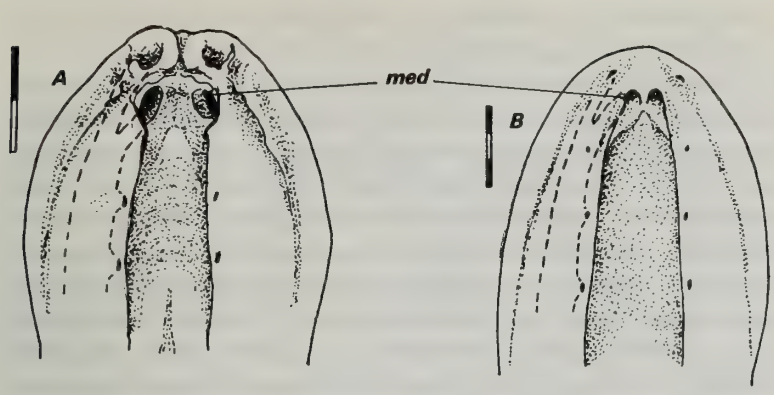

Fig. 31 Mandibular pores of A, *Ogilbia cayorum*; B, *Sirembo imberis*.

DISCUSSION

Specializations of *Acanthonus*

Acanthonus possesses a series of uniquely derived inter-linked osteological, myological and neurological cranial features. It has a lower jaw-palatine bite, a consequence of the lateral shift of the palatopterygoid articulation by outward curvature of the quadrate, in turn laterally shifted through outward curvature of the dorsal region of the hyomandibular. The relocation of the anterior hyomandibular strut has necessitated the hyomandibularis nerve piercing the anterior lamina of the bone rather than the strut itself. The preoperculum gives additional rigidity to the quadrate by its widened horizontal limb. The loss of upper jaw biting strength is reflected in the reduction of adductor muscle A1b whereas the increased importance of lower jaw-opercular series coupling is reinforced by hypertrophy of the *dilatator operculi* muscle.

Howes (1989) hypothesised that the loss of a trigeminal chamber in gadiforms was a response to increased buccal expansion so giving more freedom of passive movement to the nerve tracts. That hypothesis is here extended to the similar condition in *Acanthonus* where expansion of the buccal cavity is indicated and also accompanied by loss of a trigeminal chamber.

Nielsen (1966) commented on the biology of *Acanthonus* and examined stomach contents of six specimens, the majority of which contained crustaceans and dorsal filt of polychaetes. Another specimen, however, contained bones of a conspecific. In the three specimens here examined (310, 290, 240 mm TL) the stomach contents contained a 'mush' in which only crustacean elements are discernible.

Horn *et al.* (1978) reported on the large size of the cranial cavity of *Acanthonus* and the fact that it was filled with a low-density fluid. The authors hypothesised that since the head is the heaviest part of the body, the concentration of positively buoyant fluid provides lift and allows the fish to maintain a horizontal position with minimum swimming energy. Horn *et al.* suggest that the head might function as an acoustic dome. Certainly the cranial wall is exceedingly thin and the labyrinth is, compared with other ophidiforms (and gadiforms), extensive (Fig. 11). The fluid in which the brain is bathed is retained in the cranium by the membrane covering the large common optic-olfactory-trigeminal opening.

Compared with other ophidiiforms *Acanthonus* appears to have a relatively poorly developed olfactory system, the olfactory tract being thin and the nasal rosette having only five or six lamina (cf. 8–18 in other taxa examined (Fig. 32A). Only *Tauredophidium* and *Typhlonus* have reduced nasal rosettes with six laminae (Fig. 32B). In nearly all the specimens of *Acanthonus* available the nasal rosette is missing; since it is small and firmly attached to the connective tissue surrounding the nasal opening it appears to have become detached with the skin during collecting (the specimens are all badly damaged). In the two type specimens of *A. armatus* the rosettes are clearly visible in only one specimen (BMNH 1967.18.7:58). In the type specimen of *Typhlonus nasus* the nasal rosette is attached to and surrounded by fatty tissue. In *Xyalecyba* the nasal 'rosettes' appear to be in the form of three pear-shaped plates. Of the other taxa examined most have large nasal rosettes bearing ten–twelve laminae (Fig. 32C), *Monomitopus* and *Genypterus* both have eighteen and *Spectrunculus* has in excess of twenty (Fig. 32D), *Dicrolene* and *Glyptophidium* have the lowest number, *viz* eight.

Compared with most other ophidiiforms the eyes of *Acanthonus* are small (9.1–9.7% of head length) and the *recti* muscles are thin (Fig. 27); the lens is large and surrounded by a ring of pigment. Of 23 genera in which the eye/head length proportion has been calculated, only three approach the ratio of *Acanthonus: Genypterus, Dinematichthys* and *Tauredophidium*. In the two former genera the ratio is equal to or slightly less than that of *Acanthonus*, respectively, 6.8–8.2 and 9.0–9.8% of head length. The relatively small ratio in *Genypterus* is a reflection of its disproportionately elongate skull due to the lengthened parasphenoid ascending process and pterosphenoid (Fig. 10A). *Tauredophidium* has an eye diameter/head length ratio of 5.0% (the eye is covered with skin). In the majority of genera the proportional range is 10.3% (*Sirembo*) – 24.6% (*Lepophidium*); mode, 20.9% of head length. This range includes *Xyelacyba* (12.5 & 13.9% in the two specimens measured).

Scales are lacking in all six specimens of *Acanthonus* examined but according to Nielsen (1966), small, thin, cycloid scales occur on the head and body. Mats of sponge spicules were found associated with all the specimens, in the orbital cavities, gill chambers and mouths. The spicules apparently belong to a hexactinellid of the family Pheronematidae which tend to carpet extensive areas of the substrate in parts of the north Atlantic; these sponges play host to many invertebrates (S. Stone, pers. comm.). It is perhaps not an artefact of capture that the fishes are covered with sponge spicules but that they actively feed within the sponge beds and even bite through the sponge basket, which may be one explanation for the derived palatine-lower jaw bite.

Horn *et al.* (1978) surmise that *Acanthonus* conforms to Childress & Nygaard's (1973) hypothesis that deep-sea fishes conserve energy and discourage predation. They point out that the enlarged head of the fish and a correlated large mouth allow a wide size-range of prey. It does not necessarily follow that an expanded mouth is a correlate of an enlarged cranium (cf. the large-headed, small-mouthed macrouroids, *Echinomacrurus* and *Squalogadus*) and in *Acanthonus* it is not simply the capacity of the mouth but its derived function (lower jaw-palatine bite) which presumably further widens its prey spectrum (see above).

Relationships of *Acanthonus* and the classification of ophidiiforms

Cohen & Nielsen (1978) placed *Acanthonus* in the neobythitine tribe Sirembini along with *Sirembo, Hoplobrotula,* *Tauredophidium, Dannevigia* and *Xyelacyba*. Of these genera I have examined all except *Dannevigia* and find that *Tauredophidium* and *Xyelacyba* are closest to *Acanthonus* in overall morphology with a long, stout ventroposterior preopercular spine, a preopercular-opercular ligament covering the articulation of the operculum, a narrow operculum, occlusion between the palatine and lower jaw teeth and a 'platform' articulation between the preoperculum and quadrate and narrow operculum. *Tauredophidium* also possesses a short, single ethmoid spine (contrary to Cohen & Nielsen, 1978) but a spine is lacking in *Xyelacyba*. A superficial and radiographic examination of *Xyelacyba* suggests that although lacking an ethmoid spine it more closely resembles *Acanthonus* than does *Tauredophidium* in the morphology of its suspensorium, palatoquadrate and the first neural arch. *Hoplobrotula* also possesses an ethmoid spine (Machida, 1990), lacking in *Sirembo*, but both share an almost identical pelvic-hyoid morphology where the medial section of the *sternohyoideus* is well-separated from the lateral parts and the urohyal is reduced to a small triangular element. These are also specialized characters possessed by *Acanthonus*. Despite these apparent synapomorphies I would agree with Cohen & Nielsen's (1978) doubt that their Sirembini is a natural assemblage, since *Acanthonus* lacks the synapomorphic condition of the RLA-PP of *Sirembo* and *Hoplobrotula* and also possesses the derived external branching of the supraorbital trunk of the trigeminal nerve.

The other neobythitine division, Neobythitini, was characterized by Cohen & Nielsen (1978) solely on the basis of pelvic fin position (at the level of the preoperculum) and it includes *ca* 30 genera of which 12 have been examined. None of the characters reviewed here appear to be synapomorphic for this sample of genera and it seems unlikely that the Neobythitini as presently construed is monophyletic.

The characters described above and the limited number of taxa examined do not permit an in-depth evaluation of the existing classification of ophidiiforms (Cohen & Nielsen, 1978). They certainly uphold the division of Ophidiinae and Brotulinae. Modification of pelvic and pectoral girdle structure, associated musculature and innervation, urohyal morphology and swimbladder-vertebral association characterize the former group (six of the eight included genera have been examined). The path of the hyoideus branch of the facial nerve through the hyomandibular characterizes the Brotulinae (*Brotula* only). The Brotulinae shares derived features with several other taxa, e.g. narrow optic-olfactory foramen and separate medial section of *sternohyoideus* muscle with *Hoplobrotula, Sirembo* and *Dicrolene*, and hyomandibular flange for hyoideus branch of VII with the former; frontals contacting the pterosphenoid with *Sirembo* and *Dinematichthys*; and forward position of the forebrain with *Monomitopus* (the latter is most likely a convergent character since both taxa have short neurocrania).

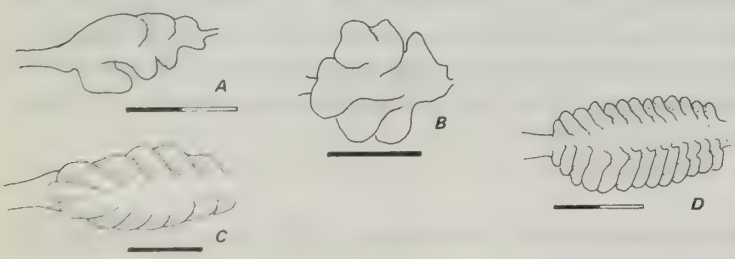

Fig. 32 Nasal rosettes of A, *Acanthonus armatus*; B, *Tauredophidium hextii*; C, *Ophidion rochei*; D, *Spectrunculus grandis*. Viewed as *in situ*, posterior to the left.

Cohen & Nielsen (1978) established a classificiation of ophidiiforms in which two orders, Ophidioidei and Bythitoidei were distinguished primarily on their respective oviparity and viviparity and secondarily on the position of the anterior nostril, either well or just above the upper lip. As pointed out by Patterson & Rosen (1989) the bythitoid characters are probably apomorphic, whereas the ophidioid ones are plesiomorphic. Within the Ophidioidei were included the Carapidae and Ophidiidae. The former have been dealt with most recently by Markle & Olney (1990) who have discovered synapomorphies which reaffirm the family's monophyly. These authors did not specifically address the problem of carapid relationships and merely point out that the Carapidae does not appear as '. . . an obvious sister group' to any other ophidiiform lineage. The Carapidae appear to be the sister-group to other ophidiiforms on the basis of their possessing a smaller, shallower exoccipital but which, like other ophidiiforms excludes the supraoccipital from the foramen magnum. Like brotulines, some neobythitines and ophidiines, carapids possess enlarged anterior epipleural ribs, similarly modified swimbladders and a well-developed basioccipital cavity with a corresponding ventromedial process on the first centrum; paired ventro-lateral processes on the lateral ethmoid articulating with the palatine, all features which characterise Ophidiiformes.

The Ophidiidae are diagnosed by Cohen & Nielsen (1978) on two plesiomorphic features: a supramaxilla and presence of body scales and on the dorsal fin rays being equal to or longer than the anal rays. This latter feature was used principally to distinguish the Ophidiidae from the Carapidae but as equal length dorsal and anal fin rays occur amongst bythitoids it is not a diagnostic character.

Of their four subfamilies the Ophidiinae and Brotulinae are clearly united on shared anatomical features of the pectoral girdle and hyoid musculature (Cohen & Nielsen, 1978; this paper). The other two subfamilies are Brotulotaeniinae, characterized by derived squamation and spinous gill-rakers (in other osteological characters it appears plesiomorphic) and Neobythitinae, diagnosed on plesiomorphic features (i.e., absence of ophidiine characters).

The Bythitoidei comprises two families, Bythitidae and Aphyonidae, the latter characterized by absence of scales and swimbladder, reduced eyes and other generally neotenic features. The Bythitidae comprises two subfamilies, Bythitinae and Brosmophycinae recognised respectively by the continuity or separation of the caudal with the dorsal and anal fins. Part of the Brosmophycinae (recognised as a tribe, Dinematichthyini) seems well characterized by a synapomorphic intromittent organ (in males) having 'ossified' elements. Of the two members of the Brosmophycini examined, *Brosmophyciops* is most like the Dinematichtyinae in its anterior vertebral column and swimbladder morphology. *Lucifuga* does not, on the basis of its vertebral column-swimbladder anatomy, appear to be closely related to *Brosmophyciops*, nor for that matter, to the group which includes the deep-water taxa (Group 2 above). Of the characters discussed in this text, the Aphyonidae retain the plesiomorphic states. A swimbladder is absent, which must certainly represent secondary loss since it is present in virtually all other ophidiiforms. However, the derived morphology of the opercular and hyoid bones supports Cohen & Nielsen's (1978) recognition of aphyonid monophyly.

In the three aphyonid genera examined, *Aphyonus, Barathronus* and *Nybelinella*, the interoperculum is reduced to a narrow strip of bone having nearly the same width as the ligament connecting it to the mandible (Fig. 33). The interopercular-mandibular ligament is elongate, twice or more the length of that in other ophidiiforms (cf. Fig. 33B). Posteriorly, the interoperculum is connected to the interhyal by connective tissue and a short, strong ligament. Distally, the interhyal is also syndesmotically connected to the tip of the posterohyal and the entire junction of the posterohyal-interhyal-interoperculum is wrapped in thin connective tissue; proximally the interhyal is attached to the posterior medial border of the preoperculum (Fig. 33A). The suboperculum is also apparently reduced but its shape cannot be readily discerned in the non-cleared and stained specimens dissected. In all these features aphyonids differ from other ophidiiforms where the interoperculum is deep, triangular or boomerang-shaped; the interopercular-mandibular ligament short and the interhyal distally connected with the posterior half of the interoperculum and with the posterohyal, and proximally attached to the central region of the preoperculum (Fig. 33B).

The majority of ophidiiform taxa are contained in the non-monophyletic Neobythitinae and Bythitidae, the former containing *ca* 50 genera, the latter *ca* 28 (Cohen & Nielsen, 1978). According to Patterson & Rosen (1989) these two assemblages could be distinguished on the basis of differences in their cranial-vertebral articulation, that of bythitids being derived. As discussed above (p. 111) this is a doubtful synapomorphy and is not supported by the synapomorphies identified here (hypertrophy of the RLA-PPD nerve (p. 122), branching of the supraorbital trigeminal trunk external to the trigeminal foramen (p. 104), and vertebral-swimbladder interconnections). These features also support a major dichotomy of ophidiiforms but different to that proposed by Patterson & Rosen (1989); Table 1.

Those taxa (except for two, see below) with the derived form of RLA-PPD (Group A) have the plesiomorphic, internal branching of the superficial-trigeminal nerve trunks while those with the derived external branching pattern (Group B) possess the plesiomorphic pelvic nerve condition. Taxa of Group A comprise the Ophidiinae (*sensu* Cohen & Nielsen, 1978) and Brotulinae (*Brotula*). The 'neobythitines' *Hoplobrotula, Sirembo, Neobythites* and *Dicrolene* display an intermediate connection of nerve branching (p. 105) and *Hoplobrotula, Sirembo* and *Dicrolene* also share derived features which indicate that they form a monophyletic group (Fig. 34). In turn they share a similar, apparently derived, mandibular sensory canal pore pattern with ophidiines (p. 126). The taxa belonging to Group B contains those other taxa presently assigned to the Neobythitinae (of the Ophidiidae) and the Bythitidae.

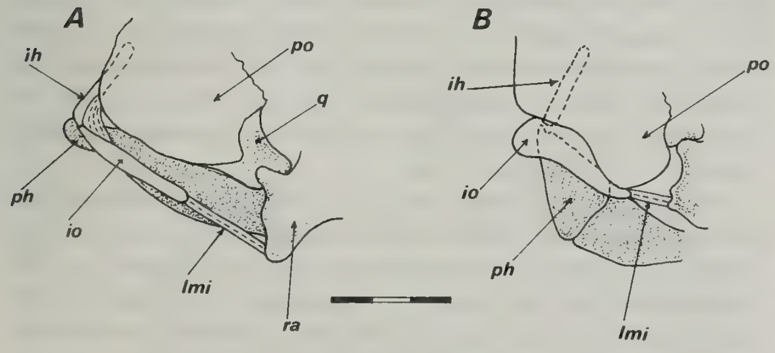

Fig. 33 Interoperculum and its associations in A, *Barathronus bicolor* (dissected specimen, lateral view); B, *Monomitopus metriostoma* (cleared and stained specimens, right lateral view).

Table 1 Group membership of the genera examined. **Group A**. RLA-PP nerve hypertrophied, exposed laterally and ventrally; some taxa with modified cleithrum and urohyal; supraorbital trunk of trigeminal primitively dividing within the cranium; anteromedial mandibular pore openings small. **Group B**, RLA-PP normal; cleithrum and urohyal unmodified; supraorbital trunk of trigeminal dividing external to facialis foramen; anteromedial mandibular pore openings usually large. **Group 1**, swimbladder anteriorly situated, intimately associated with expanded first-third (epipleural) ribs the first of which occurs on the first centrum, swimbladder often with modified anterior cap and with muscle attachment; first neural arch short. **Group 2**, swimbladder posteriorly situated, not associated with anterior ribs which are unexpanded, the first of which occurs on the third centrum (pleural); swimbladder not modified but with muscle attachment; first neural arch reduced and autogenous.

Abbreviations: X = 'intermediate' condition; O = features of these groups absent; ? = condition unknown. Under 'Present classification', A = Aphyonidae, B = Bythitoidei, N = Neobythitinae, O = Ophidiidae.

Groups	A	B	1	2	Present classification
Abyssobrotula		+		+	N
Acanthonus		+		+	N
Barathrodemus		+		+	N
Bassozetus		+		+	N
Bathyonus	+	+		+	N
Brosmophyciops		+	+		B
Brotula	+		+		O
Cataetyx		+		+	N
Cherublemma	+		+		O
Dicrolene	X	X	+		N
Diplacanthopoma		+		+	B
Genypterus	+		+		O
Glyptophidium		+	+		N
Hoplobrotula	X	X	+		N
Hypopleuron[1]	+	+	+		N
Lamprogrammus		+	+		N
Lepophidium	+		+		O
Lucifuga		+	X	X	B
Monomitopus		+	+		N
Neobythites	X	X	+		N
Ogilbia		+	+		B
Ophidion	+		+		O
Parophidium	+		+		O
Petrotyx	?	?	+		N
Penopus		+		+	N
Porogadus		+		+	N
Pycnocraspedum	?	?	+		N
Sirembo	X	X	+		N
Spectrunculus	+	+		+	N
Aphyonidae:					
Aphyonus	O	O	O	O	A
Barathronus	O	O	O	O	A

[1] *Hypopleuron* has a normal RLA-PP and the supraorbital trunk divides primitively within the trigeminal chamber so that although the taxon belongs to Groups A and B it lacks the derived features of those groups.

The neobythitine *Hypopleuron* and the bythitoid Aphyonidae possess neither of these derived characters. Loss of epipleural ribs places the Aphyonidae with Group B taxa.

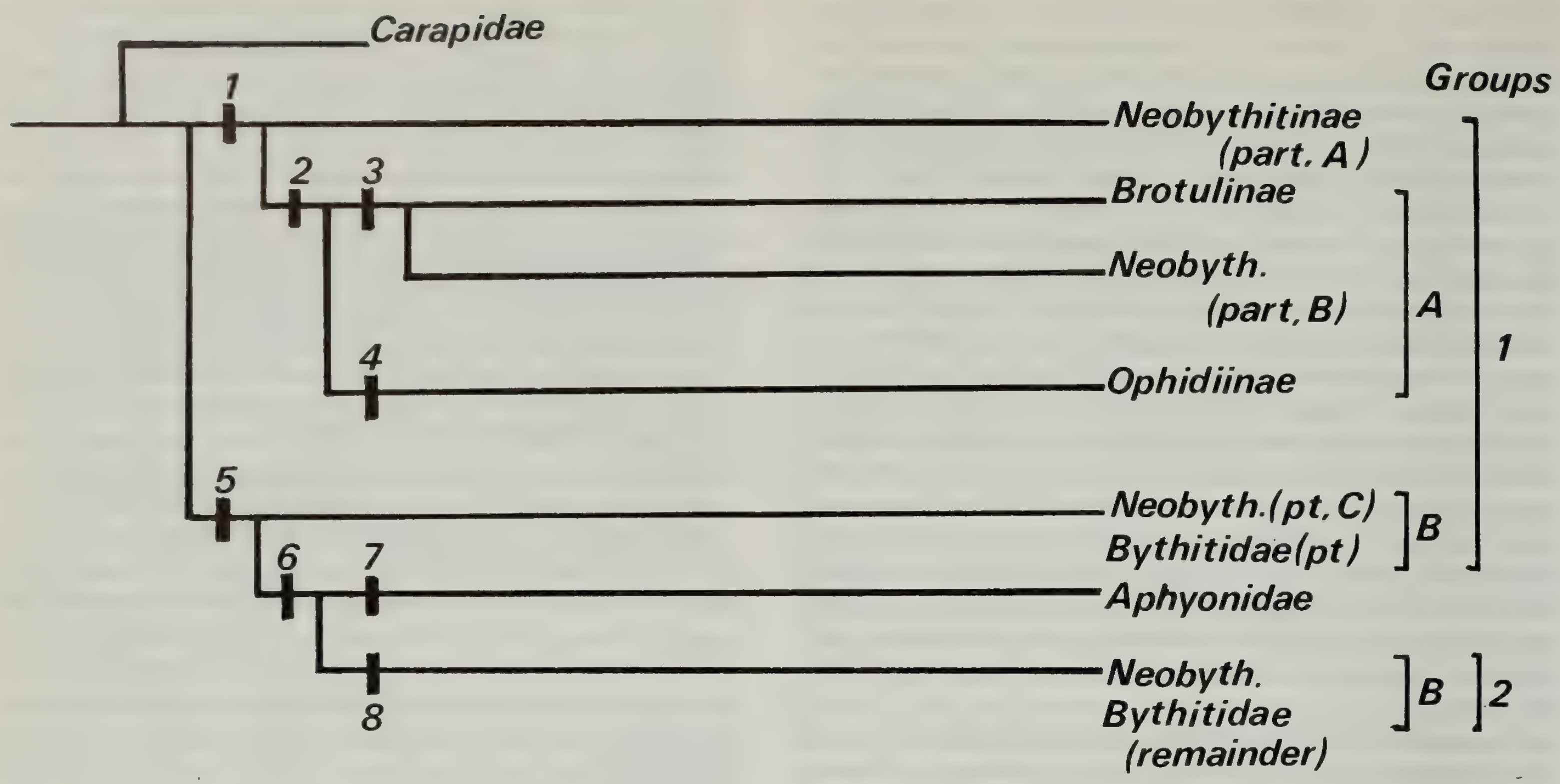

Fig. 34 Distribution of synapomorphies among investigated taxa and their correspondence with the groupings given in Table 1. The Carapidae are indicated as being the sister-group to other ophidiiforms on the basis of their sharing an enlarged exoccipital which excludes the supraoccipital from the foramen magnum but which still allows the dorsal part of the supraoccipital to form the posterior margin of the skull. They also share the ophidiiform features of expanded anterior ribs, modified swimbladder and associated muscles, basioccipital-vertebral articulation and well-developed paired lateral ethmoid facets (see text). **Synapomorphies:** 1) exoccipital dorsally expanded to exclude supraoccipital from forming the dorsoposterior cranial border; 2) RLA-PP nerve hypertrophied and exposed ventrally to hypaxial muscles; 3) olfactory-optic nerve foramen reduced to narrow aperture; separation of medial part of *sternohyoideus* muscle (occurs convergently in *Acanthonus*); enlarged mandibular sensory pores; 4) anteriorly extended cleithra; urohyal canopy-like with modified course of RLA-PP and VSR3 nerves; *pharyngohyoideus* muscle expanded; 5) supraorbital trunk of trigeminal nerve complex dividing externally to facialis chamber; 6) reduction or loss of anterior ribs; 7) opercular bones modified; 8) first neural arch reduced and autogenous; swimbladder situated posteriorly.

Neobythitinae (part A) = *Hypopleuron*; (part B) = *Hoplobrotula, Sirembo, Dicrolene*: (part C) = *Monomitopus, Lamprogrammus, Glyptophidium*; Bythitidae (part) = *Brosmophyciops*.

Groups 1 and 2 characterised on the basis of (divergently) derived swimbladder-vertebral connections correspond for the most part with the A and B groupings. Most taxa of Group 2 also belong to Group B and an overlap between Groups 1 and B occurs only amongst five genera, *biz. Brosmophyciops, Glyptophidium, Lamprogrammus, Monomitopus* and *Ogilbia* (Table 1). Membership of both Groups A and B is restricted to two genera, *Bathyonus* and *Spectrunculus*. Both possess the respective derived conditions of these groups, namely, hypertrophy and ventral exposure of RLA-PP nerve and external division of the supraorbital trunk of the trigeminal complex. Both are also members of Group 2 having the derived conditions of rib loss and posterior placement of the swimbladder. Since these genera lack any synapomorphies which characterise ophidiines, brotulines and the few 'neobythitine' genera included in Group A, it must be assumed that the RLA-PP nerve characters have been evolved independently. The division between ophidiods and bythitoids made by Cohen & Nielsen (1978) on the basis of ovo- and viviparity is transgressed by two genera, *Brosmophyciops* and *Ogilbia* both of which, by virtue of their anteriorly situated swimbladder and expanded ribs belong to Group 1. These and the aphyonids apart, the viviparous taxa are included within that assemblage possessing external branching of the supraorbital-trigeminal nerves, namely, Group B.

The 'neobythitine' *Hypopleuron* stands phylogenetically apart from other taxa in lacking any of the synapomorphies recognised here. The majority of taxa referred to the Neobythitinae and Bythitidae belong to a derived assemblage whose sister-group is the Aphyonidae, characterised by mostly reductive features (see above). The distribution of synapomorphies and their correspondence with the groups recognised above as A, B, 1 and 2 are shown in Fig. 34.

As an aside, it may be pointed out that the arrangement of caudal fin muscles in ophidiiforms correspond more closely to those of pediculate paracanthopterygians and acanthopterygians than to gadiforms. Howes (1991a) noted that gadoids have 'reduced' caudal muscles insofar as a superficial *interradiales, hypochordal longidorsalis, flexores dorsales* and *ventrales* are lacking. Ophidiiforms possess all these muscles, albeit that the superficial *interradiales* are reduced to a thin band of widely spaced fibres.

Regrettably, this study has not conclusively resolved the phylogenetic relationships of *Acanthonus* but available character data from *Tauredophidium* and *Xyelacyba* (p. 128) suggest that the three taxa form a monophyletic group. As yet the anatomy of *Tauredophidium* and *Xyelacyba* is too imperfectly known to resolve the trichotomy. The shared features of hyoid muscle anatomy and an ethmoid 'spine' which indicate relationship of *Acanthonus* and *Tauredophidium* with *Hoplobrotula* and *Sirembo* are doubtful in the light of the distribution of the trigeminal and pelvic nerve characters. No synapomorphy has emerged from this study which can further distinguish separate groups from within the larger body of taxa (in terms of the number investigated here) placed in Groups B and 2 (Fig. 34).

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Morphology and morphogenesis of the soil ciliate *Bakuella edaphoni* nov. spec. and revision of the genus *Bakuella* Agamaliev & Alekperov, 1976 (Ciliophora, Hypotrichida)

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SYNOPSIS. The morphology and morphogenesis of the hypotrichous ciliate *Bakuella edaphoni* nov. spec. from a soil in Qingdao, China, are described by observation of living and protargol impregnated specimens. The morphogenesis of cell division does not significantly differ from that of *B. salinarum*. *Bakuella* Agamaliev & Alekperov, 1976 comprises 6 species: *B. marina* Agamaliev & Alekperov, 1976 (type species), *B. crenata* Agamaliev & Alekperov, 1976, *B. edaphoni* nov. spec., *B. kreuzkampii* nov. spec., *B. salinarum* Mihailowitsch & Wilbert, 1990, and *B. walibonensis* nov. spec. *Bakuella imbricata* Alekperov, 1982 and *B. polycirrata* Alekperov, 1988 are junior synonyms of *B. marina* and *B. crenata*, respectively. *Bakuella agamalievi* Borror & Wicklow, 1983, *B. variabilis* Borror & Wicklow, 1983, and *B. pulchra* (Buitkamp, 1977) Jankowski, 1979, do not belong to the genus *Bakuella*. The obliquely arranged ventral rows behind the midventral cirri and the 3 enlarged frontal cirri could place the genera *Bakuella* and *Parabakuella* Song & Wilbert, 1988 in the subfamily Bakuellinae Jankowski, 1979, within the family Holostichidae Fauré-Fremiet, 1961.

INTRODUCTION

Agamaliev & Alekperov (1976) established the genus *Bakuella* for two new hypotrichous ciliates with short, obliquely arranged cirral rows at the posterior end of the midventral row. Since then new representatives of this genus have been described by Alekperov (1982, 1988), Borror & Wicklow (1983), and Mihailowitsch & Wilbert (1990). A further new species is here described, the morphology and morphogenesis of which have been examined in detail. The genus *Bakuella*, which now contains 6 species from saline water, freshwater, and soil, is revised.

MATERIALS, METHODS, AND TERMINOLOGY

Bakuella edaphoni inhabits the upper soil layer (0–2 cm) on a hill in the city of Qingdao, China (36° 08' N; 120° 43' E). Excystation occurred about 3 days after the incubation of the air-dried soil was begun (for method see Buitkamp, 1977). Some individuals were taken from this initial culture and transferred to petri dishes containing Eau de Volvic as culture medium, with a few crushed wheat grains to promote bacterial growth.

The infraciliature was revealed by the protargol impregnation method according to Wilbert (1975). All counts and measurements were made at a magnification of ×1500. The drawings of the protargol impregnated specimens were made with a camera lucida. For clarity, in the morphogenic stages of *B. edaphoni*, the parental cirri are shown only by outline, whereas new ones are shaded. The terminology is according to Kahl (1932), Borror (1972), Borror & Wicklow (1983), Corliss (1979), Foissner (1982), and Hemberger (1982). Wiackowski (1985, 1988) designates both the zigzag arranged ventral cirri and the short rows posteriad of them as midventral cirri, which is correct in terms of morphogenesis. However, the term 'midventral row' is here used only for the sum of the zigzag arranged ventral cirri (= midventral cirri). The more or less obliquely arranged short rows are designated as ventral rows. For details of the morphometrical analysis see Berger et al. (1984).

DESCRIPTION OF *BAKUELLA EDAPHONI* NOV. SPEC.

DIAGNOSIS. *In vivo* 190–300 × 50–85 µm. More than 100 macronuclear segments. 7 buccal cirri, 3 frontoterminal cirri, 8 transverse cirri, 9 pairs of midventral cirri, 7 ventral rows, and 39 adoral membranelles on average.

TYPE LOCALITY. Upper soil layer on a hill in the city of Qingdao, China.

TYPE MATERIAL. The slide of holotype specimens and 1 slide of paratype specimens are deposited in the collection of microscopic preparations of the College of Fisheries, Ocean University of Qingdao, China. 1 paratype slide (reference number 1990:11:19:1) is deposited in the Natural History Museum, London.

DESCRIPTION (Figs 1–5, Table 1). Long elliptical, posteriorly distinctly narrowed. About 2:1 dorsoventrally flattened, flexible. Macronuclear segments ellipsoidal, rather regularly distributed in cytoplasm. 2–7 ($\bar{x}$ = 4.6, SD = 2.0, Vr = 43%, n = 16) micronuclei. Contractile vacuole at level of cytostome (Fig. 1). Cortical granules absent. Cytoplasm colourless, often densely packed with up to 5 µm large, colourless globules (mitochondria?), readily visible after protargol impregnation (Fig. 3). Feeds on bacteria, diatoms, zooflagellates, testaceans, and small ciliates. Moderately rapid movement.

Buccal area large. 1–7, usually 2 or 3, cirri immediately posterior to right frontal cirrus (Fig. 4, arrow). Midventral row terminates at about level of cytostome. Anterior ventral rows with 3–5 cirri, posterior rows with 7–14 cirri each. Both marginal rows terminate in median of cell without overlapping (Figs 1, 4).

COMPARISON WITH RELATED SPECIES. *Bakuella edaphoni* differs from the type species (Figs 21–35) in habitat and in that it has more buccal cirri and fewer frontoterminal cirri (Table 1). *Bakuella salinarum* has distinctly more pairs of midventral cirri and only 2 frontoterminal cirri (Fig. 41). In *B. kreuzkampii* and *B. walibonensis* the ventral rows are few in number and rather short (Figs 51, 52). Furthermore, both species have only 2 frontoterminal cirri. Recently, P. Eigner & W. Foissner (pers. comm. to H. Berger) found a rather similar terrestrial species which has, however, conspicuous cortical granules (visible *in vivo* and after protargol impregnation!) arranged in longitudinal rows. At superficial *in vivo*

Table 1 Morphometrical characterization of *Bakuella agamalievi* (aga, uncertain species, from Agamaliev, 1972; wet silver impregnation), *B. crenata* (cre, from Agamaliev & Alekperov, 1976; wet silver impregnation), *B. edaphoni* (eda, original data; protargol impregnation), *B. kreuzkampii* (kre, from Mihailowitsch & Wilbert, 1990; protargol impregnation), *B. marina* (ma1, from Agamaliev & Alekperov, 1976; wet silver impregnation. ma2, original data of the population of Wilbert, 1986; protargol impregnation. ma3, *B. imbricata* from Alekperov, 1982; wet silver impregnation. ma4, original data; protargol impregnation), *B. salinarum* (sal, from Mihailowitsch & Wilbert, 1990; protargol impregnation), and *B. walibonensis* (wal, from Mihailowitsch & Wilbert, 1990; protargol impregnation). All measurements in µm. ? = sample size unknown; if only 1 value is known it is listed in column $\bar{x}$, if 2 values are available they are listed as Min and Max. Max = maximum value; Min = minimum value; n = number of individuals examined; SD = standard deviation; Vr = coefficient of variation in %; $\bar{x}$ = arithmetic mean.

Character	Species	$\bar{x}$	SD	Vr	Min	Max	n
Body, length	aga	–	–	–	140	220	?
	cre	–	–	–	120	150	?
	eda	219.6	41.5	18.9	153	283	16
	kre	155.8	16.4	10.5	136	176	5
	ma1	–	–	–	120	140	?
	ma2	266.7	27.6	–	230	310	25
	ma3	–	–	–	110	130	?
	ma4	101.4	5.7	–	91	108	18
	sal	307.4	26.6	8.6	272	348	10
	wal	202.0	16.3	8.0	180	229	10
Body, width	eda	69.4	8.1	11.7	59	82	16
	kre	46.6	4.0	8.6	40	51	6
	ma2	85.0	14.8	–	70	110	11
	ma4	61.6	6.3	–	45	70	18
	sal	99.1	18.6	18.7	87	145	10
	wal	72.3	8.5	11.7	62	83	7
Adoral zone of membranelles, length	eda	62.8	10.9	17.4	47	82	16
Adoral membranelles, number	aga	–	–	–	25	30	?
	cre	–	–	–	28	30	?
	eda	38.9	2.8	7.3	34	45	16
	kre	33.7	2.3	6.8	30	37	7
	ma1	–	–	–	32	36	?
	ma2	40.4	4.2	–	34	51	25
	ma3	–	–	–	38	40	?
	ma4	32.4	2.4	–	28	36	12
	sal	55.4	5.1	9.2	47	63	10
	wal	39.2	4.1	10.5	33	47	17
Frontoterminal cirri, number	cre[1]	10.0	–	–	–	–	1
	eda	3.1	0.8	24.3	2	5	22
	kre	2.0	–	–	2	2	7
	ma1	9.0	–	–	–	–	?
	ma2	7.6	2.0	–	5	11	27
	ma3	9.0	–	–	–	–	?
	ma4	6.7	1.0	–	5	9	14
	sal	2.0	–	–	2	2	10
	wal	2.0	–	–	2	2	17
Buccal cirri, number	cre	–	–	–	3	4	?
	eda	7.4	1.3	17.7	5	9	24
	kre	1.0	–	–	1	1	7
	ma1	–	–	–	3	4	?
	ma2	3.1	0.9	–	2	5	34
	ma3	–	–	–	4	5	?
	ma4	2.2	0.5	–	2	4	9
	sal	7.1	0.9	12.3	6	8	10
	wal	5.8	0.4	17.2	5	6	17

Character	Species	x̄	SD	Vr	Min	Max	n
Midventral row, number of pairs of cirri	aga	–	–	–	5	7?	?
	cre[1]	5.0?	–	–	–	–	1
	eda	9.5	2.3	24.1	5	14	24
	ma1	12.0?	–	–	–	–	?
	ma2	9.8	4.7	–	4	12	22
	ma3	–	–	–	4	8	?
	ma4	4.4	0.3	–	4	5	18
	sal	26.0	7.9	30.4	22	38	7
	wal	13.8	0.4	3.0	13	14	15
Number of ventral rows with 3 cirri	cre[1]	3.0?	–	–	–	–	1
	eda	2.6	1.0	37.0	1	5	22
	kre	14.0	2.6	18.6	10	18	7
Number of ventral rows with more than 3 cirri	cre[1]	7.0	–	–	–	–	1
	eda	4.5	0.7	16.6	3	6	22
Total number of ventral rows	cre[1]	10.0	–	–	–	–	1
	eda	7.1	1.3	18.1	5	10	22
	kre	3.6	1.0	27.8	3	5	7
	ma1	10.0	–	–	–	–	?
	ma2	7.0	0.8	–	5	8	16
	ma3	–	–	–	5	7	?
	ma4	4.3	0.5	–	4	5	15
	sal	15.8	2.9	18.4	13	21	10
	wal	2.6	1.2	44.6	2	5	12
Transverse cirri, number	aga	5.0	–	–	–	–	?
	cre[1]	7.0	–	–	–	–	1
	eda	8.0	1.5	18.3	6	11	16
	kre	5.3	1.0	18.9	5	7	7
	ma1	10.0	–	–	–	–	?
	ma2	7.0	1.6	–	5	11	27
	ma3	7.0	–	–	–	–	?
	ma4	7.2	1.4	–	5	9	20
	sal	9.5	2.2	22.8	7	12	10
	wal	5.2	0.7	13.1	4	6	15
Right marginal row, number of cirri	aga	–	–	–	28	30	?
	cre	–	–	–	40	45	?
	eda	50.6	4.1	8.1	43	55	10
	kre	41.0	5.2	12.7	34	46	6
	ma1	–	–	–	55	60	?
	ma2	44.4	7.6	–	34	63	23
	ma3	–	–	–	40	42	?
	ma4	40.7	5.6	–	34	54	9
	sal	62.2	5.7	9.2	55	66	10
	wal	60.5	6.3	10.4	51	66	11
Left marginal row, number of cirri	aga	38.0	–	–	–	–	?
	cre	–	–	–	38	40	?
	eda	48.4	3.7	7.6	44	56	10
	kre	37.6	4.5	12.0	30	40	7
	ma1	–	–	–	52	56	?
	ma2	35.9	9.0	–	23	53	23
	ma3	–	–	–	32	35	?
	ma4	28.3	2.7	–	25	33	9
	sal	51.7	5.2	10.0	45	60	10
	wal	51.5	4.5	8.8	42	50	13
Dorsal kineties, number	cre[2]	2.0?	–	–	–	–	?
	eda	3.0	0	0	3	3	24
	kre	3.0	0	0	3	3	7
	ma2	3.0	0	–	3	3	12
	ma3	3.0	–	–	–	–	?
	ma4	3.0	0	–	3	3	25
	sal	3.0	0	0	3	3	10
	wal	3.0	0	0	3	3	17

[1] From Fig. 38.

[2] See taxonomy of this species.

observation *B. edaphoni* can be easily confused with large *Holosticha* species (Foissner, 1982). The soil species *Paraurostyla pulchra* Buitkamp, 1977, which was probably erroneously transferred to the genus *Bakuella* by Jankowski (1979), almost certainly has no midventral cirri (Fig. 53).

MORPHOGENESIS OF CELL DIVISION (Figs 6–20).

The first event in morphogenesis is the formation of small groups of basal bodies close to the posterior end of the middle ventral rows (Fig. 6) and near the left transverse cirrus (Fig. 7, arrow). The basal bodies increase in number forming a longish field from which some migrate forward to the posterior portion of the midventral row (Fig. 8). The parental endoral membrane and the anterior third of the paroral membrane dedifferentiate (Fig. 8, small arrows). Simultaneously the posterior buccal cirri are modified to the anlage II of the proter (Fig. 8, large arrow). The pharyngeal fibres disappear. The macronuclear segments fuse to about 15 ellipsoidal segments with reorganization bands.

The adoral membranelles of the opisthe develop in a posteriad direction (Fig. 9, large arrow). At this stage some of the posterior cirri of the middle ventral rows are dedifferentiated and the posterior portion of the paroral membrane becomes disorganized. Between the dedifferentiated buccal row and the unaltered midventral row some small rows of basal bodies occur (Fig. 9, small arrows). The macronuclear segments differ in size.

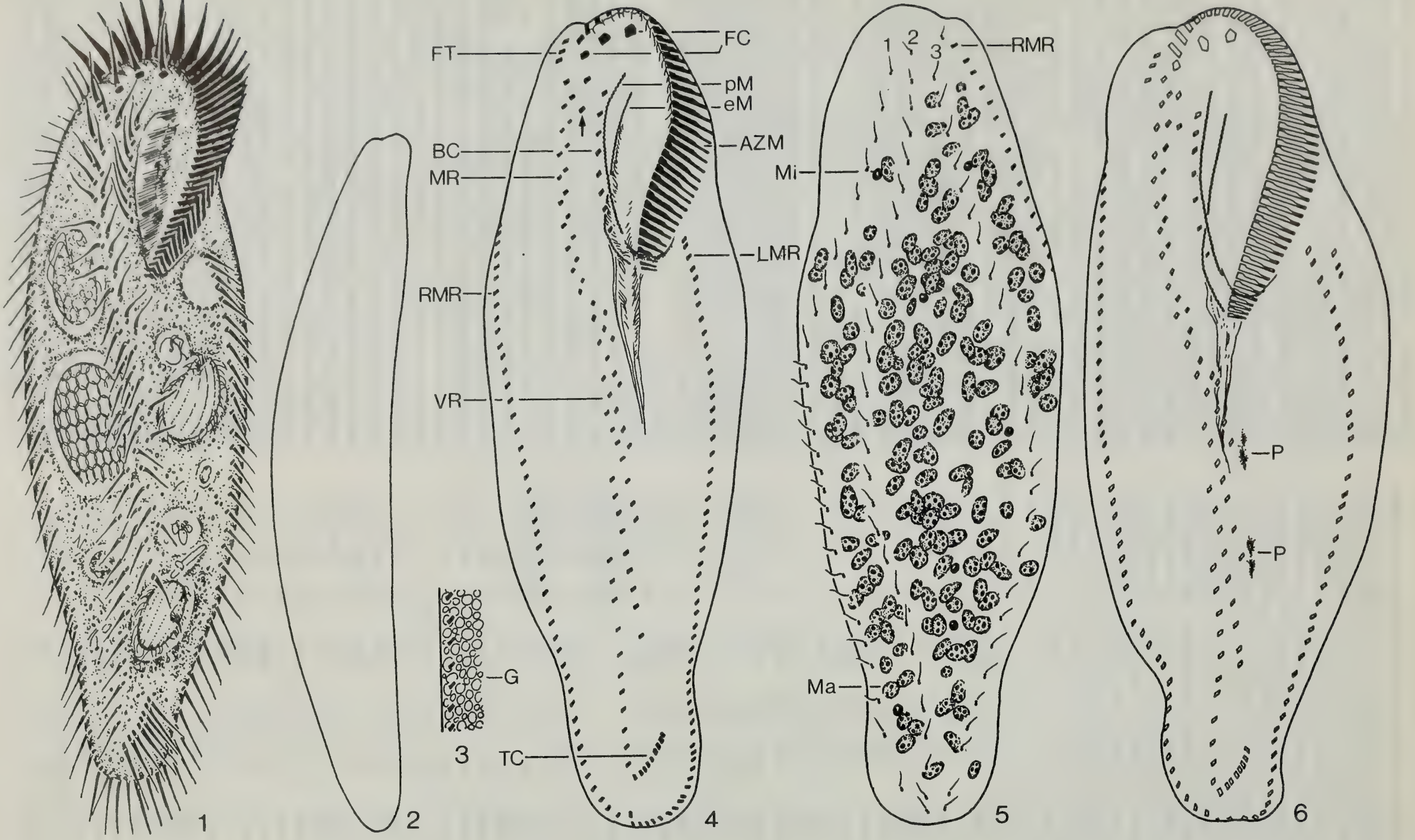
In the middle stages of morphogenesis most of the cirri of the ventral rows are modified to primordia of the opisthe. The parental buccal cirri are now a narrow band (Fig. 10, arrow). Some midventral cirri are obviously incorporated in the formation of the obliquely arranged primordial streaks. In both the marginal rows and in all dorsal kineties 2 primordia occur (Figs 10, 11). The macronucleus is a large single mass.

Somewhat later the proximal parental adoral membranelles begin with reorganization. Possibly the posterior end of the anlage I of the proter is involved in this process (Fig. 12, small arrow). Both in the proter and in the opisthe, about 20 short anlagen and the new left frontal cirrus (Fig. 12, large arrows) are recognizable.

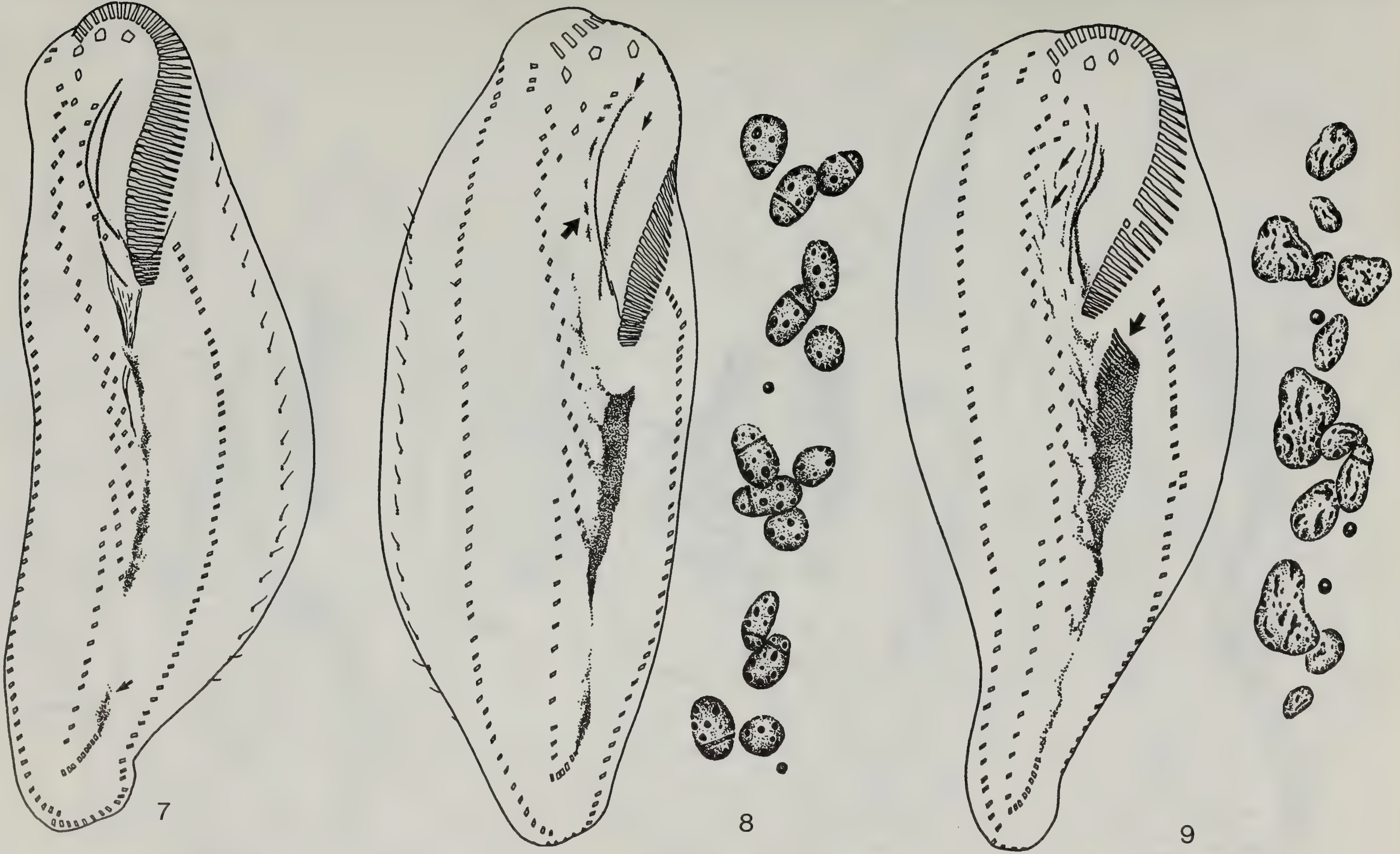
In the next stage the oral primordium of the opisthe is already distinctly bent to the right and completely modified to adoral membranelles (Fig. 13). The reorganization of the parental adoral zone of membranelles is restricted to about 10 proximal membranelles. In both the proter and the opisthe the numerous obliquely arranged streaks begin with the differentiation of cirri. The large arrows in Fig. 13 mark the penultimate streaks. These streaks appear to form the frontoterminal cirri (Figs 13, 15) although this is unusual because, in general, the frontoterminal cirri originate from the anterior part of the posteriormost anlage. The morphogenesis of the dorsal infraciliature shows no peculiarities. The macronucleus and the micronuclei begin to divide (Fig. 14).

Figure 15 and 16 show a late morphogenetic stage. All new fronto-ventral-transverse cirri are differentiated and they begin to migrate to their final positions. Immediately before the separation of the proter and the opisthe, most of the parental cirri and dorsal kineties are resorbed (Figs 17, 18). The morphogenesis of the dorsal infraciliature shows unequivocally that no caudal cirri are present (Fig. 18).

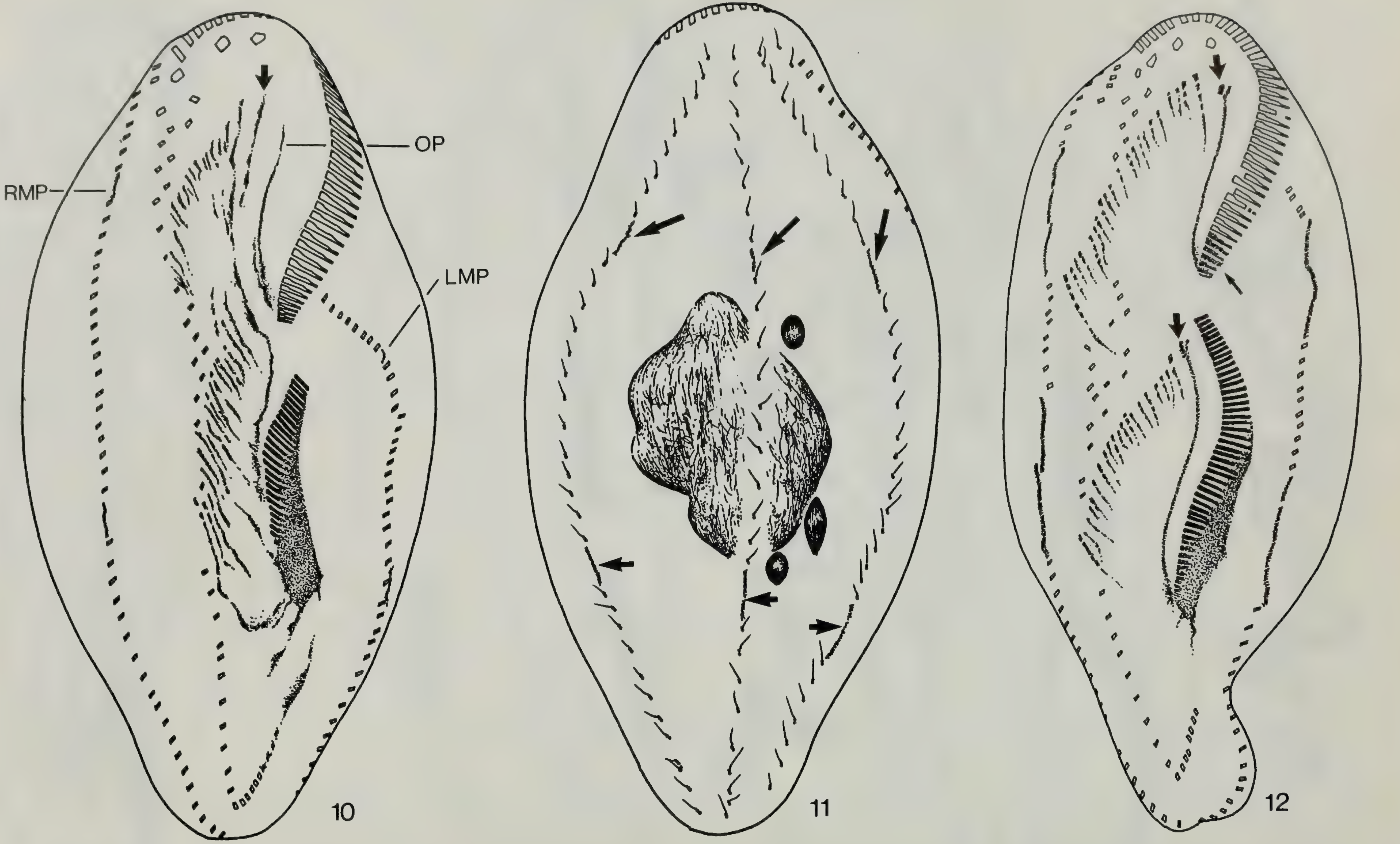
The postdividers have a wide elliptical outline (Figs 19, 20). Now the pharyngeal fibres impregnate again. The macronucleus commences with segmentation. In



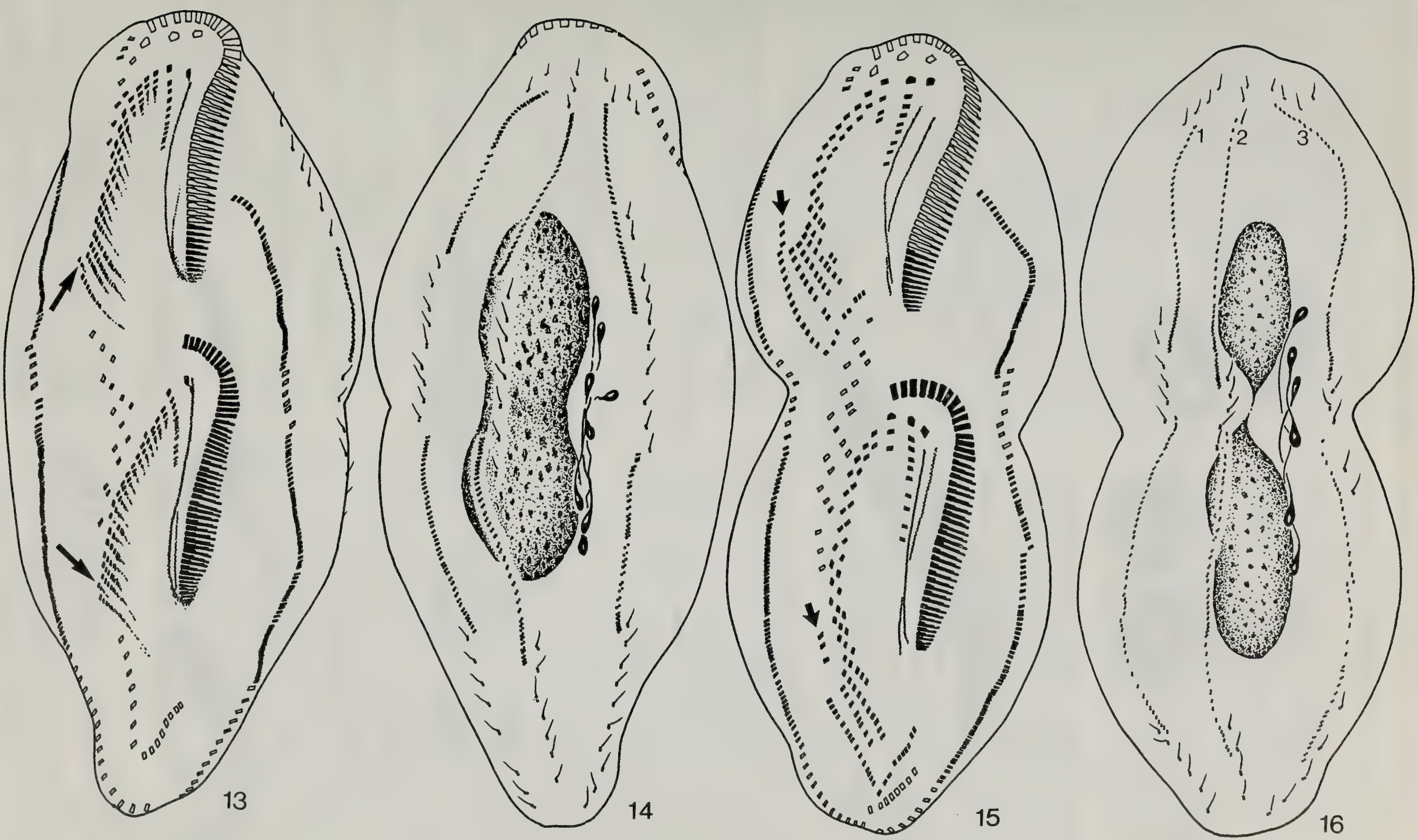
Figs 1-6 *Bakuella edaphoni* nov. spec. (1–6, originals. 1, 2, *in vivo*; 3–6, protargol impregnation). **1, 2** Ventral and lateral views, 225 µm, 215 µm. **3** Part of the pellicle to show the densely packed, up to 5 µm in diameter, globules (mitochondria?). **4, 5** Infraciliature in ventral and dorsal view, 240 µm. The arrow in Fig. 4 marks the cirri behind the right frontal cirrus. **6** Very early morphogenetic stage in ventral view, 280 µm. AZM = adoral zone of membranelles; BC = buccal cirri; eM = endoral membrane; FC = frontal cirri; FT = frontoterminal cirri; G = endoplasminal granule; LMR = left marginal row; Ma = macronuclear segment; Mi = micronucleus; MR = midventral row; P = oral primordium of the opisthe; pM = paroral membrane; RMR = right marginal row; TC = transverse cirri; VR = ventral rows behind the midventral row; 1-3 = dorsal kineties 1-3.



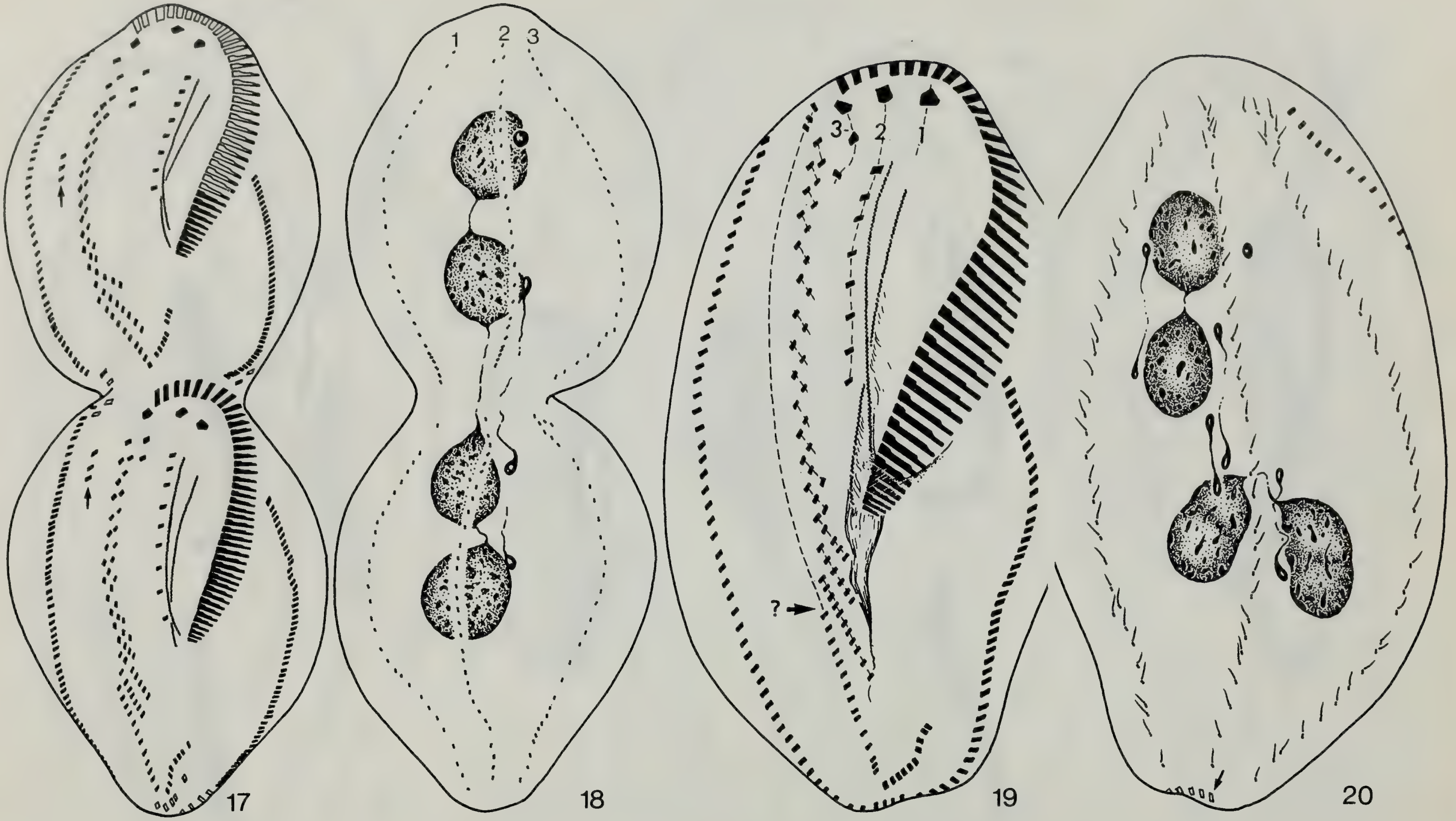
Figs 7-9 *Bakuella edaphoni* nov. spec. (7–9, originals. Morphogenetic stages in ventral view after protargol impregnation). **7** Very early stage, 275 µm. The arrow marks the primordium close to the transverse cirri. **8** Early stage, 250 µm. Small arrows, dedifferentiated endoral and paroral (only the anterior part) membrane; large arrow, dedifferentiated buccal cirri. **9** Early stage, 250 µm. Large arrow, formation of the adoral membranelles of the opisthe; small arrows, primordia of the fronto-ventral-transverse streaks.



Figs 10-12 *Bakuella edaphoni* nov. spec. (10–12, originals. Morphogenetic stages after protargol impregnation). **10** Middle stage in ventral view, 200 µm. Large arrow, anlage II of the proter. **11** Middle stage in dorsal view, 200 µm. The arrows mark the primordia of the new dorsal kineties. **12** Middle stage in ventral view, 270 µm. Large arrows, new left frontal cirrus of the proter and the opisthe; small arrow, reorganizing proximal part of the parental adoral zone of membranelles. LMP = primordium of the left marginal row; OP = anlage I of the proter; RMP = primordium of the right marginal row.



Figs 13-16 *Bakuella edaphoni* nov. spec. (13–16, originals. Morphogenetic stages after protargol impregnation). **13, 14** Middle stage in ventral and dorsal view, 220 µm. Large arrows, anlagen of the frontoterminal cirri. **15, 16** Late stage in ventral and dorsal view, 205 µm. Large arrows, new frontoterminal cirri. 1–3 = new dorsal kineties 1–3.



Figs 17-20 *Bakuella edaphoni* nov. spec. (17–20, originals. Morphogenetic stages after protargol impregnation). **17, 18** Very late stage in ventral and dorsal view, 220 µm. The arrows mark the new frontoterminal cirri. **19, 20** Postdivider in ventral and dorsal view, 120 µm. The cirri which originate from the same anlage are connected by dotted lines; the origin of the frontoterminal cirri could not be precisely determined (arrow with ?; for details see text). The arrow in Fig. 20 marks the posterior end of the left marginal row. 1–3 = anlagen I, II, and III and dorsal kineties 1–3, respectively.

Figure 19 those cirri which originate from the same streak are connected by dotted lines.

DISCUSSION. The morphogenesis does not significantly differ from that of *B. salinarum* (Figs 41–50). Mihailowitsch & Wilbert (1990) describe a complete reorganization of the parental adoral zone of membranelles. This is, however, obviously a misinterpretation. Figs 46, 47 show that, just as in *B. edaphoni* and in *Keronella gracilis* Wiackowski, 1985, only the proximal membranelles are reorganized. Figure 45 does not show a morphogenetic stage as assumed by Mihailowitsch & Wilbert (1990), but a reorganizer.

The streaks (= anlagen) of the fronto-ventral-transverse primordia in the proter have the following origin: streak I, from the parental undulating membranes; it forms the new undulating membranes and the left frontal cirrus. Streak II, from the parental buccal cirri; it forms the middle frontal cirrus and the buccal cirri. Streak III, probably *de novo*; it forms the right frontal cirrus and 1 or more cirri behind this cirrus. Streaks IV to n, probably *de novo* and by modification of parental midventral cirri, respectively (Figs 9, 10); they form the numerous cirral pairs of the midventral row, the ventral rows, and the transverse cirri. The origin of the frontoterminal cirri could not be unequivocally recognized (Fig. 19, arrow with '?'). It gives the impression that they originate from the last but one streak which is, however, not in accordance with any other morphogenetic pattern of related species (Fig. 13). In the opisthe streaks I-n are derived from the oral primordium and modified ventral rows (Figs 8–10).

The morphogenesis of the dorsal infraciliature proceeds as in *B. salinarum* and e.g. in *Kahliella franzi* (Foissner, 1982) Berger & Foissner, 1988 or *Gonostomum strenua* (Engelmann, 1862) Sterki, 1878 (see Song, 1990), viz. according to type 1 of Foissner & Adam (1983).

REVISION OF THE GENUS *BAKUELLA* Agamaliev & Alekperov, 1976

Bakuella Agamaliev & Alekperov, 1976

1976 *Bakuella* Agamaliev & Alekperov, Zool. Zh., 55: 128 – Type species (original designation): *Bakuella marina* Agamaliev & Alekperov, 1976.

1977 *Bakuella* Agam. & Alek. – Corliss, Trans. Am. microsc. Soc., 96: 137 (see nomenclature and taxonomy).

1979 *Bakuella* Agamaliev & Alekperov, 1976 – Corliss, Ciliated protozoa, p. 309.

1979 *Bakuella* Agamaliev & Alekperov, 1976 – Tuffrau, Trans. Am. microsc. Soc., 98: 526.

1979 *Bakuella* Agamaliev & Alekperov, 1976 – Jankowski, Trudӯ zool. Inst., Leningr., 86: 50.

1979 *Bakuella (Bakuella)* Jankowski, Trudӯ zool. Inst., Leningr., 86: 50 – Type species (original designation): *Bakuella marina* Alekperov & Agamaliev, 1976.

1979 *Bakuella (Loxocineta)* Jankowski, Trudӯ zool. Inst., Leningr., 86: 51, 57 – Type species (original designation): *Bakuella crenata* Alekperov & Agamaliev, 1976.

1983 *Bakuella* Agamaliev & Alekperov, 1976 – Borror & Wicklow, Acta Protozool., 22: 113.

1985 *Bakuella* – Small & Lynn, Phylum Ciliophora, p. 450.

1987 *Bakuella* Agamaliev & Alekperov, 1976 – Tuffrau, Annls Sci. nat., 8: 115.

1989 *Bakuella* Agamaliev et Alekperov 1976 – Alekperov, Ecology of marine and freshwater protozoans, p. 7.

1990 *Bakuella* Agamaliev & Alekperov, 1976 – Mihailowitsch & Wilbert, Arch. Protistenk., 138: 208.

DIAGNOSIS. Medium sized to large Holostichidae; obliquely arranged ventral rows situated behind midventral row; 3 slightly to distinctly enlarged frontal cirri; 2 or more frontoterminal cirri; transverse cirri present; 1 left and 1 right marginal row; caudal cirri absent.

ADDITIONAL CHARACTERS. Most of the species are described only from silver impregnated material. Thus the important character of the presence or absence of cortical granulation is unknown in these species. Outline usually long elliptical, both ends rounded. Body flexible. Adoral zone of membranelles 30–40% of body length. Undulating membranes bent and crossing. Bases of transverse cirri not conspicuously enlarged. 3 dorsal kineties (possibly a generic character; a redescription of *B. crenata* following protargol impregnation will probably reveal that it also has 3 dorsal kineties; Table 1). Dorsal cilia *in vivo* 3–5 μm long. Edaphic, limnic, and marine species.

REMARKS. Corliss (1977, p. 111, 137) erroneously designated *Bakuella* as a nomen nudum. The suggestion of Jankowski (1979) that the number of macronuclear segments should be used for the splitting into the 2 subgenera *Bakuella* and *Loxocineta* does not appear to be justified.

Three other genera are known which have obliquely arranged ventral rows behind the midventral row, viz. (i) *Parabakuella* Song & Wilbert, 1988 (3 frontal cirri; transverse cirri absent; 1 left and 1 right marginal row; caudal cirri present), (ii) *Keronella* Wiackowski, 1985 (many frontal cirri, i.e. the anterior part of the midventral row, form a 'bicorona'; transverse cirri present; 1 left and 1 right marginal row; caudal cirri present; see also Wirnsberger, 1987), and (iii) *Metabakuella* Alekperov, 1989 (many frontal cirri form a 'bicorna'; transverse cirri present; 1 [or more?] right and 2 or more left marginal rows; caudal cirri absent?). Two of these genera, viz. *Bakuella* and *Parabakuella*, can be united in the subfamily Bakuellinae Jankowski, 1979 for which we propose the following improved DIAGNOSIS: Holostichidae with more or less obliquely arranged ventral rows behind the midventral row; 3 more or less distinctly enlarged frontal cirri. TYPE GENUS: *Bakuella* Agamaliev & Alekperov, 1976. Nomenclatural remarks: Jankowski (1979, p. 74) established the family Bakuellidae. According to Article 50c (i) of the ICZN (1985) a change in rank of a taxon within the family group does not affect the authorship of the name of the taxon. Thus Jankowski is the author of the subfamily Bakuellinae and not Alekperov (1988), who erroneously wrote 'subfamily Bakuellinae (Jank.) comb. n.').

KEY TO SPECIES

1 Species from terrestrial habitats .... ***B. edaphoni*** (Figs 1–20)

— Species from limnic or marine habitats 2

2 2 macronuclear segments .... ***B. crenata*** (Figs 36–40)

— Many (usually >100) macronuclear segments (e.g. Fig. 22) . 3

3 Posteriormost ventral row terminates roughly in the middle or at the end of the 2nd third of the cell; ventral rows with only about 3–4 cirri (Figs 51, 52) 4

— Posteriormost ventral row terminates at about the level of the transverse cirri; ventral rows with up to 13 cirri (e.g. Figs 21, 41) 5

4 1 buccal cirrus; an additional row between the anterior end of the midventral row and the right marginal row .... ***B. kreuzkampii*** (Fig. 52)

— 5–6 buccal cirri; no such row .... ***B. walibonensis*** (Fig. 51)

5 2 frontoterminal cirri; 22–38 pairs of cirri in the midventral row .... ***B. salinarum*** (Figs 41–50)

— 5–11 frontoterminal cirri; 4–12 pairs of cirri in the midventral row .... ***B. marina*** (Figs 21–35)

DESCRIPTION OF SPECIES

REMARKS. Characters which are mentioned in (i) the diagnosis, (ii) the section 'additional characters' of the genus, (iii) the key, or (iv) the tables, are not repeated in the descriptions below. Thus, some of them are rather short.

Bakuella crenata Agamaliev & Alekperov, 1976

1976 *Bakuella crenata* Agamaliev & Alekperov, Zool. Zh., 55: 130 (Fig. 38).

1979 *Bakuella (Loxocineta) crenata* – Jankowski, Trudȳ zool. Inst., Leningr., 86: 51.

1982 *Bakuella crenata* – Alekperov, Zool. Zh., 61: 1253.

1983 *Bakuella crenata* Agamaliev & Alekperov, 1976 – Borror & Wicklow, Acta Protozool., 22: 113.

1988 *Bakuella polycirrata* Alekperov, Zool. Zh., 67: 778 (nov. syn.; Figs 36, 37, 39, 40).

TAXONOMY. *Bakuella polycirrata* is almost certainly only a postdivider of *B. crenata* (Figs 36, 37). This is indicated by the enormous relative size of the adoral zone of membranelles (more than 50%), the unusual position of the porus of the contractile vacuole, and the immature ventral infraciliature (cp. Figs 19 and 36). The only significant difference is the number of dorsal kineties; only 2 in *B. crenata* and 5 in *B. polycirrata* (Fig. 37). This difference may be due to the wet silver impregnation method employed, which yields inaccurate data for the dorsal infraciliature (e.g., *Stylonychia mytilus* sensu Agamaliev, 1978). Another possibility is that in Fig. 37 parental dorsal kineties are still preserved. A detailed redescription of this taxon is necessary.

MORPHOLOGY (Figs 36–40, Table 1). *In vivo* (?) up to 210 µm long. Each macronuclear segment with a micronucleus. Marginal rows distinctly separated posteriorly.

OCCURRENCE. Locus classicus is the Djeiranbatansky freshwater reservoir in Azerbaijan. *Bakuella polycirrata* was found in the same (?) freshwater habitat. Not found since.

Bakuella marina Agamaliev & Alekperov, 1976

1976 *Bakuella marina* Agamaliev & Alekperov, Zool. Zh., 55: 129 (Figs 21, 22).

1979 *Bakuella (Bakuella) marina* – Jankowski, Trudȳ zool. Inst., Leningr., 86: 50.

1982 *Bakuella marina* – Alekperov, Zool. Zh., 61: 1253 (Figs 26, 27).

1982 *Bakuella imbricata* Alekperov, Zool. Zh., 61: 1253 (nov. syn.; Figs 31, 32).

1983 *Bakuella marina* A. et A., 1976 – Borror & Wicklow, Acta Protozool., 22: 113.

1983 *Bakuella marina* Agamaliev et Alekperov, 1976 – Agamaliev, Ciliates of Caspian Sea, p. 105.

1986 *Bakuella marina* Agamaliev – Wilbert, Symposia Biologica Hungarica, 33: 251 (Figs 28–30).

NOMENCLATURE AND TAXONOMY. '*Bakyella marina*' in Agamaliyev (1976, p. 91) is an incorrect subsequent spelling. *Bakuella marina* is probably the senior synonym of *B. imbricata* because the important biometric data are rather similar (cp. Figs 21, 26, 31, Table 1). *Bakuella marina* sensu Wilbert (1986) is distinctly larger. Other characters, however, agree well, so that the identification can be accepted for the time being.

MORPHOLOGY (Figs 21–35, Table 1). *In vivo* (?) about 200 µm long. Contractile vacuole porus at level of cytostome (Figs 21, 23, 26). Posterior ventral rows with up to 13 cirri (Figs 21, 24, 26, 31). Marginal rows usually distinctly separated posteriorly. Sometimes with 4 dorsal kineties (Fig. 30).

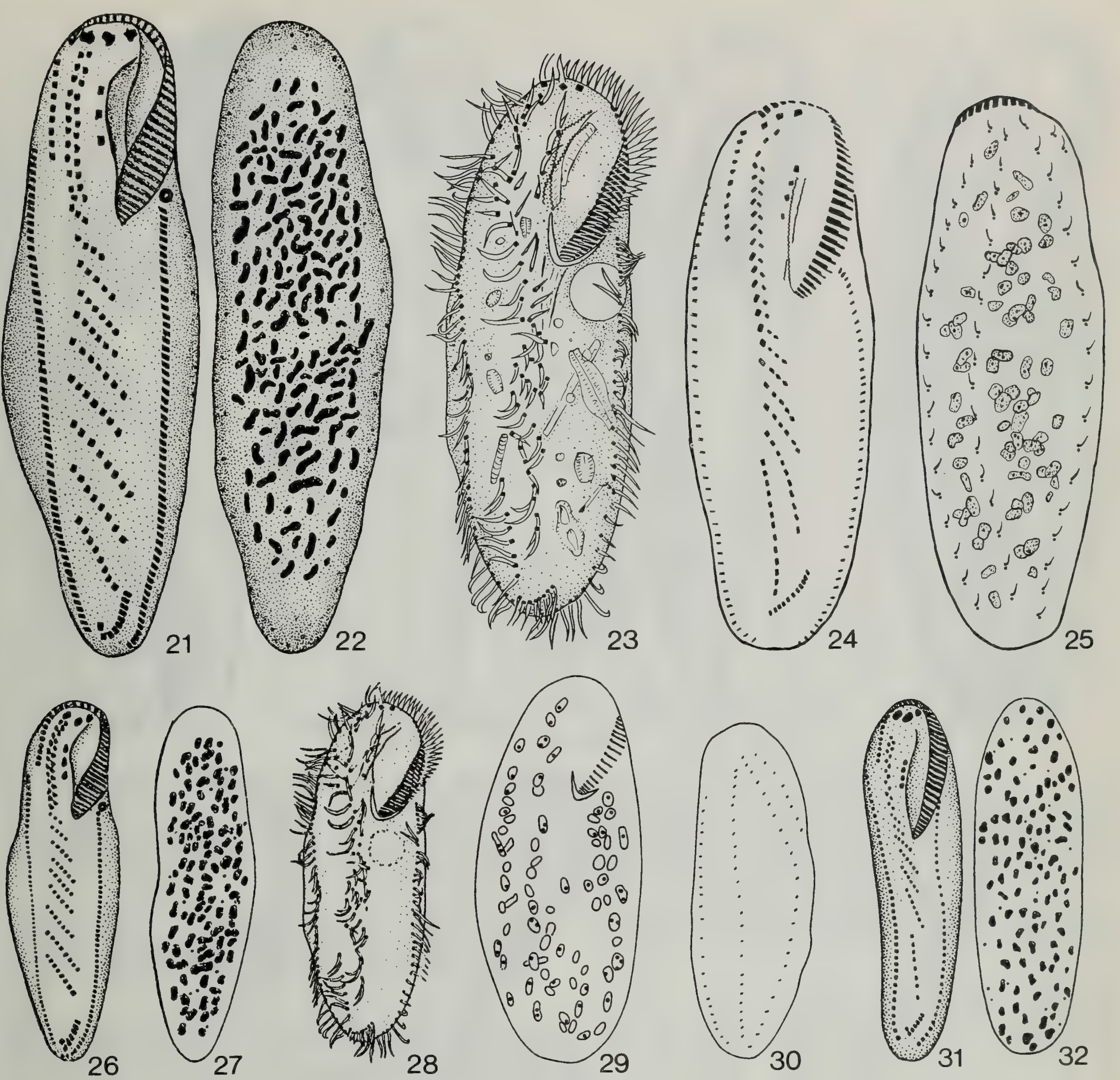
OCCURRENCE AND ECOLOGY. Locus classicus is the Caspian Sea (see also Agamaliyev, 1976). Wilbert (1986) found it in saline lakes in Saskatchewan, Canada. According to Hammer (1986) *B. marina* occurs at salinities of 2–37%. Chaouite et al. (1990) recorded it in mineral and hot springs in France. Locus classicus of the synonymous *B. imbricata* is the Djeiranbatansky freshwater reservoir, Azerbaijan.

Bakuella salinarum Mihailowitsch & Wilbert, 1990

1990 *Bakuella salinarum* Mihailowitsch & Wilbert, Arch. Protistenk., 138: 208 (holotype slide deposited in Institut für Landwirtschaftliche Zoologie und Bienenkunde, University of Bonn, Germany).

MORPHOLOGY (Figs 41–50, Table 1). *In vivo* 280–350 µm long. Contractile vacuole roughly in middle of cell. 2 micronuclei. Cells brownish (no information is given why). 2 cirri situated behind right frontal cirrus. Anteriormost buccal cirrus slightly enlarged. Midventral row terminates slightly behind middle of cell. Ventral rows rather densely arranged. Marginal rows slightly overlapping. Very probably during morphogenesis the parental adoral zone of membranelles is reorganized only proximally and not completely as supposed by Mihailowitsch & Wilbert (1990; see discussion of *B. edaphoni*).

OCCURRENCE AND ECOLOGY. Locus classicus is a salt-loaded ditch in Bad Waldliesborn, Lippstadt, Germany (for details see Mihailowitsch, 1989). Feeds on bacteria. Mihailowitsch & Wilbert (1990) give the following autecological data (n = 28): 5.3–16.3 °C, pH 7.0–7.7, 19–187 mg l^{-1} CO_2 (free), 2.2–9.6 mg l^{-1} O_2, 0.13–7.3 mg l^{-1} NH_4^+–N, 0.02–0.4 mg l^{-1}



Figs 21–32 *Bakuella marina* (21, 22, from Agamaliev & Alekperov, 1976; 23, from Wilbert, 1986 slightly modified; 24, 25, originals of a population from a saline lake in Saskatchevan, Canada; 26, 27, 31, 32, from Alekperov, 1982; 28–30, from Wilbert, 1986. 21, 22, 26, 31, wet silver impregnation; 23–25, 28–30, protargol impregnation; 27, 32, Feulgen staining). **21–32** Infraciliature in ventral and dorsal view and nucleus apparatus, 21, 22 = 120 μm, 23–25 = 230–310 μm, 26, 27 = ? μm, 28 = 210 μm, 29 = 240 μm, 30 = 212 μm, 31, 32 = 110–130 μm.

NO$_2^-$–N, 0.63–10.6 mg l^{-1} NO$_3^-$–N, 300–12763 mg l^{-1} Cl$^-$, 216–3590 mS m^{-1} spec. conductivity.

Bakuella walibonensis nov. spec.

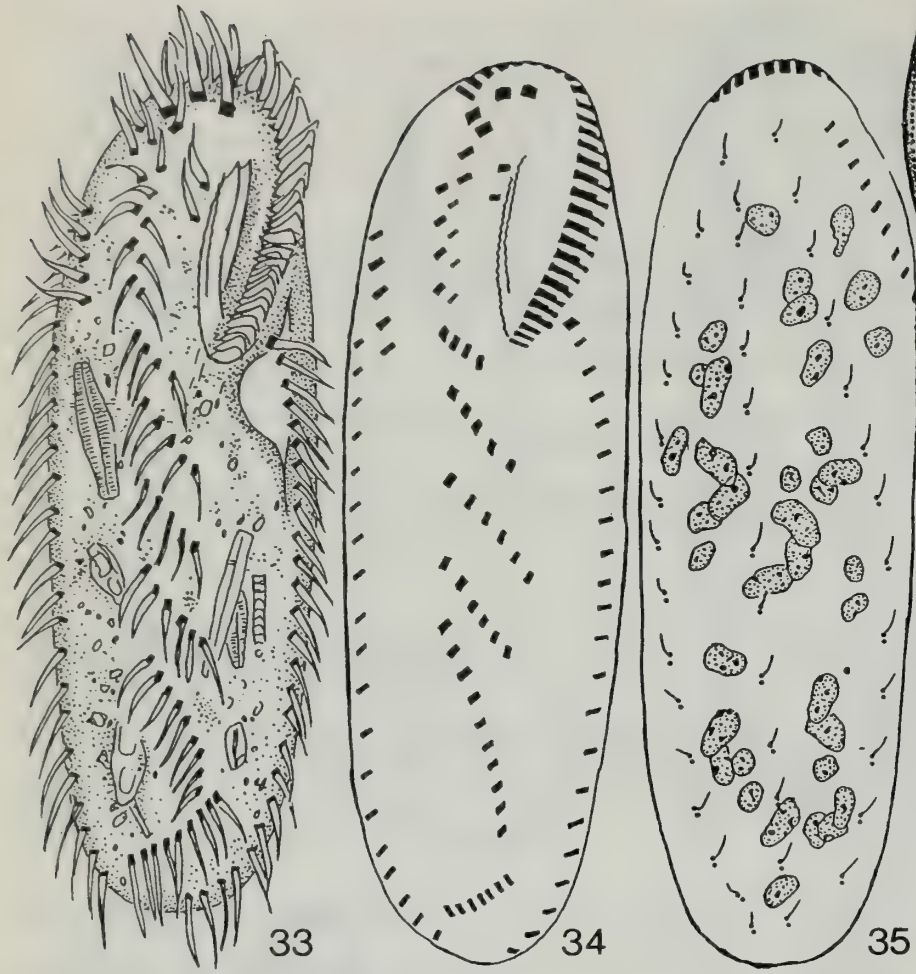
1990 *Bakuella* spec. 1 – Mihailowitsch & Wilbert, Arch. Protistenk., 138: 213.

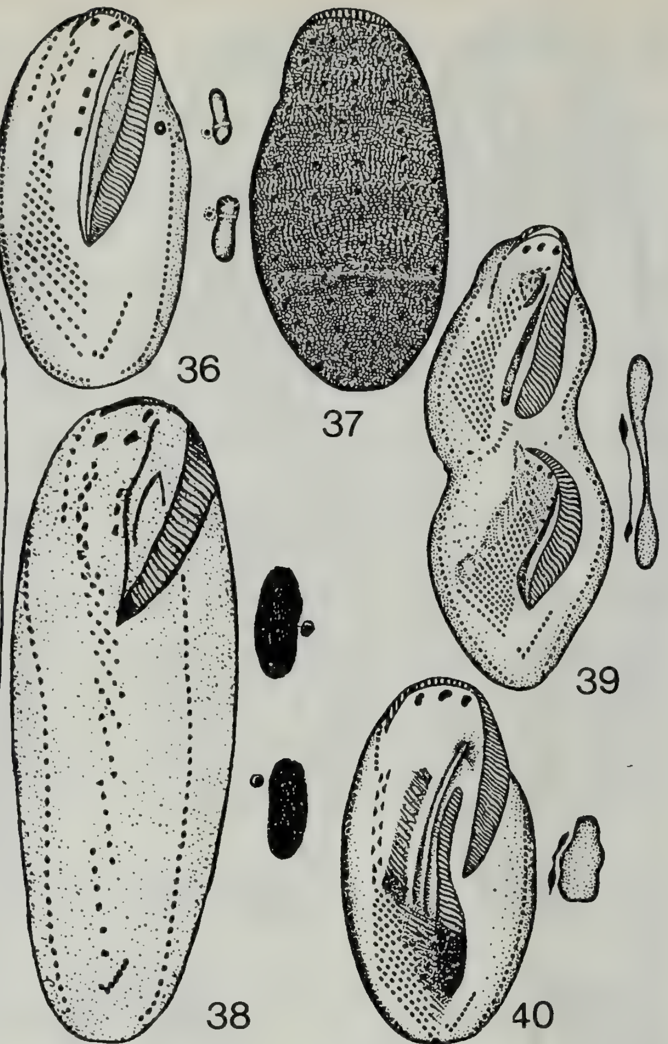
TAXONOMY. Redescription necessary, especially *in vivo* observations. Differs from the rather similar *B. kreuzkampii* (Fig. 52) in that it has more buccal cirri and no additional 'frontal' row between the anterior end of the midventral row and the right marginal row.

DIAGNOSIS. After protargol impregnation about 180–230 × 60–80 μm. More than 100 macronuclear segments. 6 buccal cirri, 5 transverse cirri, 14 pairs of midventral cirri, and 39 adoral membranelles on average. 2–5 ventral rows and consistently 2 frontoterminal cirri.

TYPE LOCALITY. Salt-loaded ditch in Bad Waldliesborn, Lippstadt, Germany.

MORPHOLOGY (Fig. 51, Table 1). Contractile vacuole situated slightly behind the middle of the cell. 3 cirri left of anterior end of midventral row. Ventral rows terminate at about level





Figs 33–35 *Bakuella marina* (originals of a population from a saline lake in Saskatchevan, Canada). **33** Ventral view *in vivo*. **34, 35** Infraciliature in ventral and dorsal view, protargol impregnation, 91–108 μm.

Figs 36–40 *Bakuella crenata* (36, 37, 39, 40, from Alekperov, 1988; 38, from Agamaliev & Alekperov, 1976. 36–40, wet silver impregnation; nuclear apparatus after Feulgen staining). **36, 37** Infraciliature of a postdivider in ventral and dorsal view, 66 μm. **38** Infraciliature in ventral view, 195 μm. **39** Late morphogenetic stage in ventral view. **40** Reorganizer in ventral view.

of contractile vacuole and marginal rows almost exactly in median of cell.

Bakuella kreuzkampii nov. spec.

1990 *Bakuella* spec. 2 – Mihailowitsch & Wilbert, Arch. Protistenk., 138: 213.

TAXONOMY. Redescription necessary, especially *in vivo* observations. The rather similar *B. walibonensis* has more buccal cirri and no cirral row between the anterior end of the midventral row and the right marginal row (Fig. 51).

DIAGNOSIS. After protargol impregnation about 135–175 × 40–50 μm. More than 100 macronuclear segments. 5 transverse cirri, 14 pairs of midventral cirri, and 34 adoral membranelles on average. 3–5 ventral rows and consistently 1 buccal cirrus and 2 frontoterminal cirri.

TYPE LOCALITY. Salt-loaded ditch in Bad Waldliesborn, Lippstadt, Germany.

MORPHOLOGY (Fig. 52, Table 1). A short row with about 6 cirri between anterior end of right marginal row and midventral row. Ventral rows terminate at about level of contractile vacuole and marginal rows almost exactly in median of cell.

UNIDENTIFIABLE TAXA AND SPECIES EXCLUDED FROM THE GENUS *BAKUELLA*

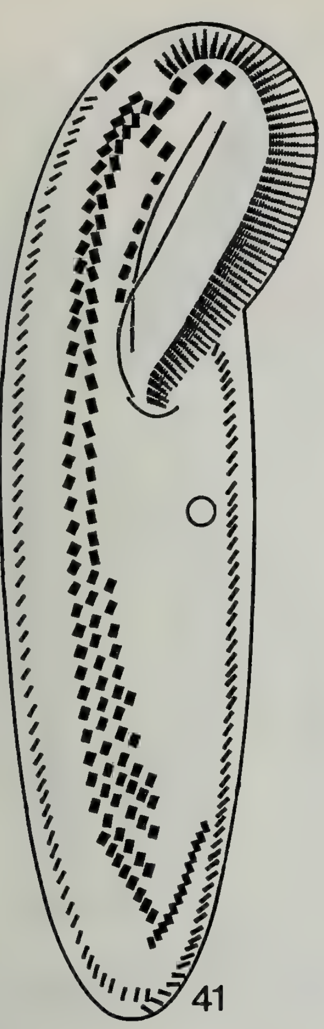
Bakuella agamalievi Borror & Wicklow, 1983

1972 *Holosticha manca* Kahl, 1932 – Agamaliev, Acta Protozool., 10: 21 (misidentification; Figs 54, 55).

1983 *Bakuella agamalievi* Borror & Wicklow, Acta Protozool., 22: 114, 117, 120.

REMARKS (Figs 54, 55, Table 1). This species was established for the rather superficially described *Holosticha manca* sensu Agamaliev (1972). Almost certainly *Keronopsis rubra* sensu Agamaliev (1974, p. 72, Fig. 10) represents the same taxon. Whilst in both descriptions buccal and frontoterminal

Figs 41–47 *Bakuella salinarum* (from Mihailowitsch & Wilbert, 1990. 41–47, protargol impregnation). **41, 42** Infraciliature of a non-dividing specimen in ventral and dorsal view, 225 μm. **43, 44** Very early and early morphogenetic stage in ventral view. **45** Reorganizer. **46, 47** Late stages in ventral view.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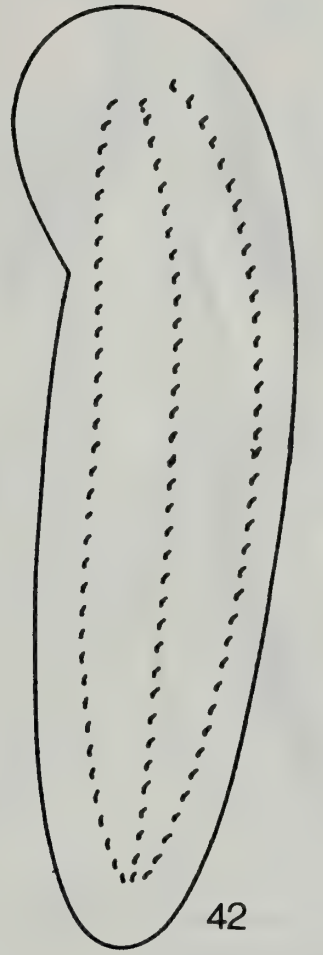
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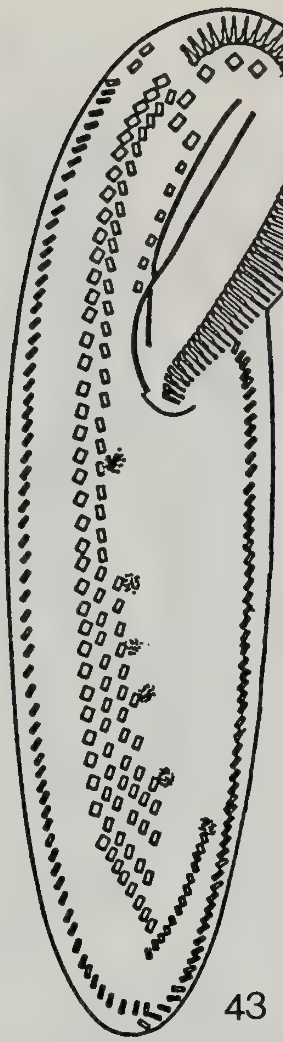
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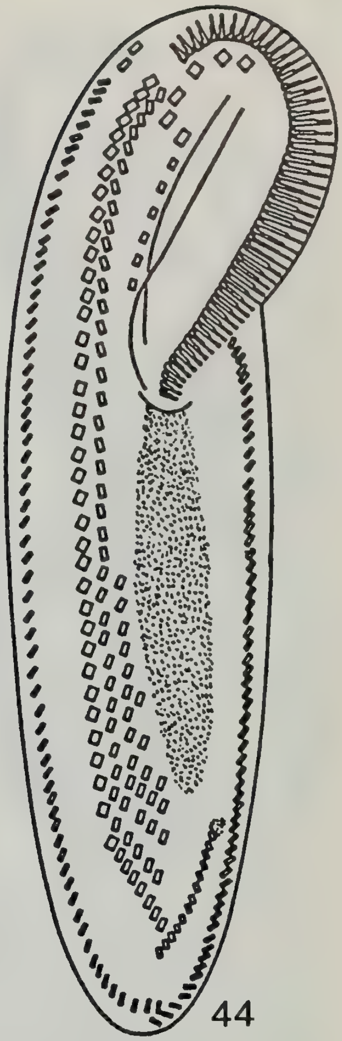
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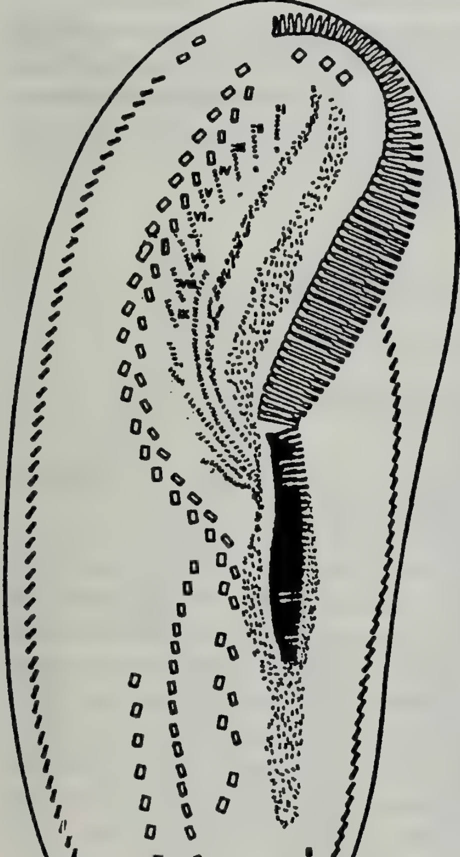
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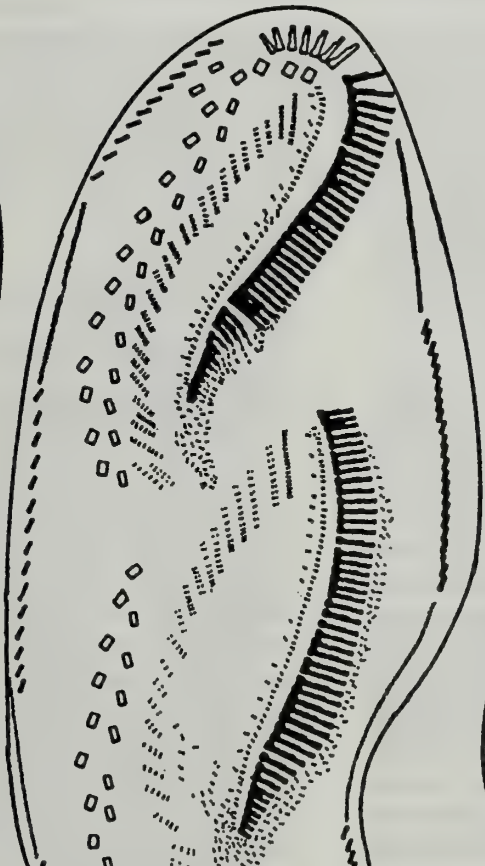
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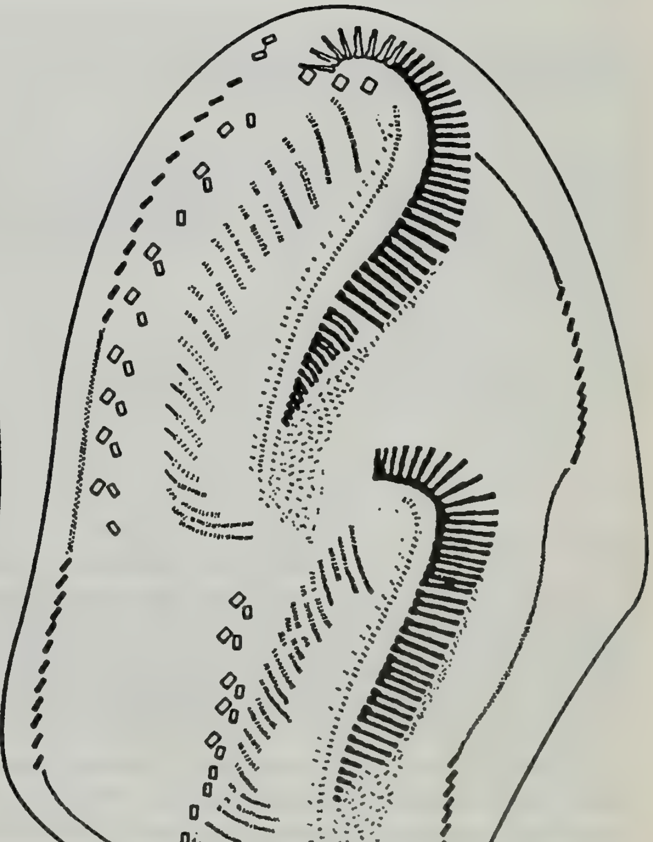
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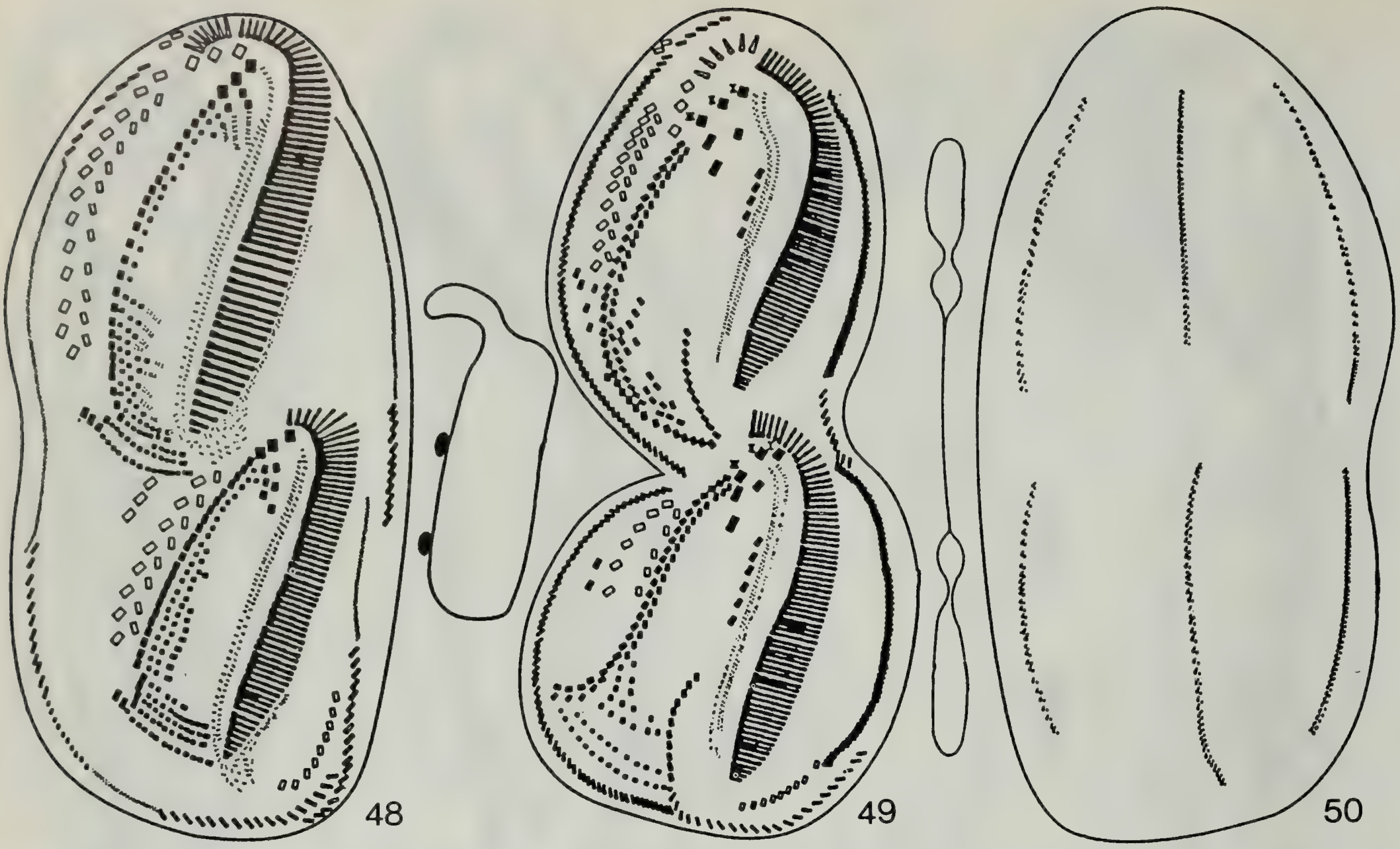


Figs 48–50 *Bakuella salinarum* (from Mihailowitsch & Wilbert, 1990. 48–50, morphogenetic stages after protargol impregnation). **48, 49** Late and very late stage in ventral view, 303 µm, 340 µm. **50** Late stage in dorsal view, 303 µm.

cirri are absent, it is assumed that they were overlooked, possibly due to the inappropriate wet silver impregnation method used. Because no ventral rows are recognizable, it must be excluded from *Bakuella*. Possibly it belongs to the genus *Holosticha*. Length about 2.5 times width. Both marginal rows terminate at level of transverse cirri. Number of dorsal kineties unknown. Locus classicus is the Caspian Sea. Not found since.

Paraurostyla pulchra Buitkamp, 1977

1977 *Paraurostyla pulchra* Buitkamp, Decheniana, 130: 119 (Fig. 53).

1979 *Bakuella pulchra* – Jankowski, Trudŷ zool. Inst., Leningr., 86: 83.

REMARKS (Fig. 53). '*Parayrostyla pulchra*' in Jankowski (1979, p. 83) is a misspelling. Its inclusion in the genus *Bakuella* is not justified, because it has no midventral row. However, there is no doubt that some other characters, such as the absence of caudal cirri, the 3 dorsal kineties, the large number of macronuclear segments, the short cirral row near the anterior end of the right marginal row which simulates the frontoterminal row, and more than 1 buccal cirrus, remind one of members of the genus *Bakuella*. Thus only a detailed redescription, including an investigation of the morphogenesis, will definitively elucidate the correct systematic position of *Paraurostyla pulchra*. Roughly spindle-shaped. Contractile vacuole slightly above middle of cell. 2 ventral cirri in front of transverse cirri, which are circa 18 µm long and only slightly enlarged. Right marginal row begins at about level of posterior buccal cirri and terminates at level of transverse cirri; left marginal row terminates in median of cell. Feeds on diatoms and ciliates. Locus classicus of *P. pulchra* is the upper soil layer (0–5 cm) of a pasture near Bonn, Germany. Not found since. Buitkamp (1979) counted 79 individuals g^{-1} dry soil 6 days after incubation at 30°C. Biomass of 10^6 individuals about 300 mg (Foissner, 1987).

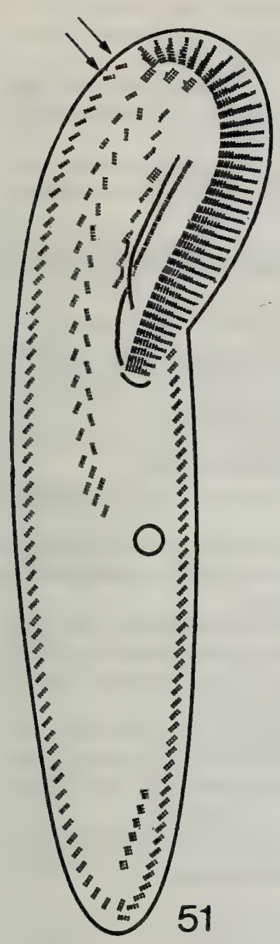
Bakuella variabilis Borror & Wicklow, 1983

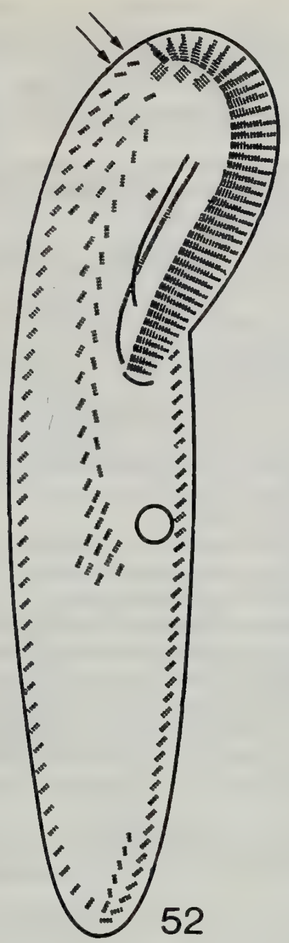
1979 ?*Bakuella* sp. – Borror, J. Protozool., 26: 547 (Fig. 56).

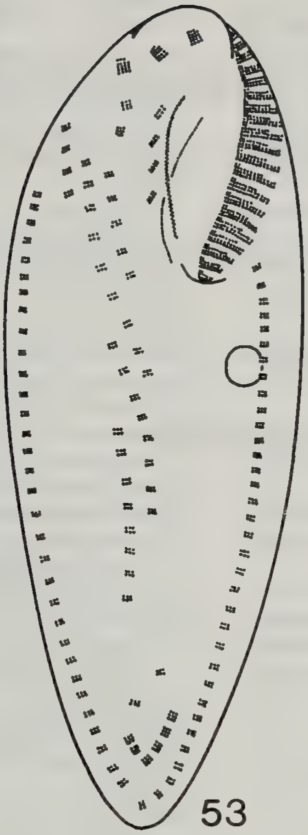
1983 *Bakuella variabilis* Borror & Wicklow, Acta Protozool., 22: 111 (Fig. 57).

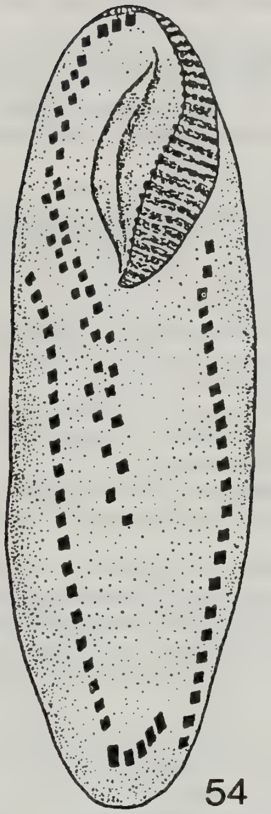
1989 *Metabakuella variabilis* (B. & W.) – Alekperov, Ecology of marine and freshwater protozoans, p. 7.

REMARKS. *Bakuella variabilis* has 2–5 left marginal rows. Furthermore, the ventral rows are rather long and are not obliquely arranged behind the midventral row as in all other species of the genus (Fig. 57). The arrangment of the ventral rows reminds strongly on *Urostyla grandis* Ehrenberg, 1830. *Urostyla*, however, has many frontal cirri which form a bicorona (see Foissner et al., 1991, Ganner, 1991). A classification in the genus *Metabakuella* is also uncertain, because the type species, *M. perbella* (Alekperov & Musayev, 1988) Alekperov, 1989, has a bicorona too. The correct generic classification of *B. variabilis* can only be determined after a detailed description of the morphogenesis. Possible it needs a genus of its own. *In vivo* 225–240 µm long. Flexible and opaque. More than 100 small macronuclear segments. Contractile vacuole at about the level of the cytostome. Cortical









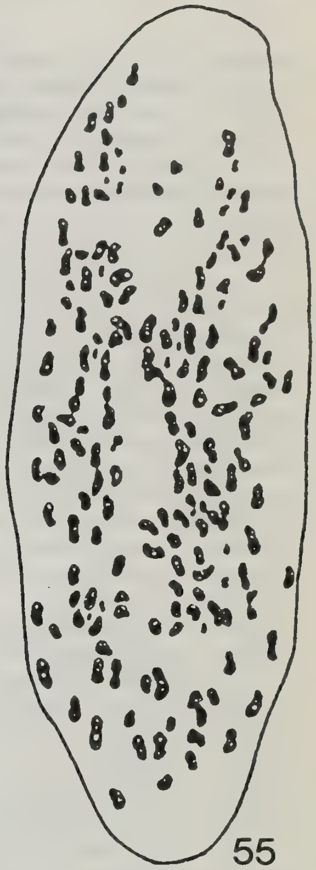


Fig. 51 *Bakuella walibonensis* nov. spec. (from Mihailowitsch & Wilbert, 1990). Infraciliature in ventral view, protargol impregnation, 165 µm. The arrows mark the frontoterminal cirri.

Fig. 52 *Bakuella kreuzkampii* nov. spec. (from Mihailowitsch & Wilbert, 1990). Infraciliature in ventral view, protargol impregnation, 165 µm. The arrows mark the frontoterminal cirri.

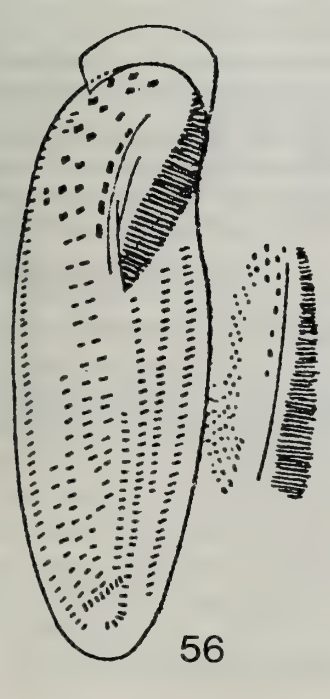
Fig. 53 *Paraurostyla pulchra* (from Buitkamp, 1977). Infraciliature in ventral view, protargol impregnation, 158 µm.

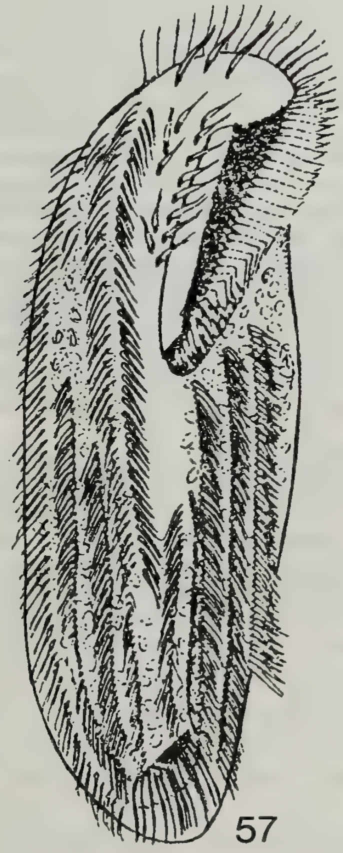
Figs 54, 55 *Bakuella agamalievi* (from Agamaliev, 1972). **54** Infraciliature in ventral view, wet silver impregnation, 95 µm. **55** Nucleus apparatus, Feulgen staining.

granules on entire surface, 2–4 granules near each cirrus, on dorsal surface oblique rows, 3–10 granules per row. Feeds on flagellates. Adoral zone of membranelles about 1/3 of body length. 3 frontal cirri, 8–10 buccal cirri, about 12 transverse cirri. 1 right marginal row. Frontoterminal cirri present. Locus classicus of *B. variabilis* is a temporary pool in a flooded agricultural field in Lee, New Hampshire, USA (70°58′ W. Long., 43°8′ N. Lat.).

Bakuella sp. in Wiackowski (1988) is not figured. Thus an identification is impossible.

Acknowledgements. We thank Prof Dr W. Foissner, University of Salzburg, for some critical comments on the manuscript. The first author wishes to acknowledge the financial support of the ‘Shandong Foundation for Natural Sciences’.





Figs 56, 57 *Bakuella variabilis* (56, from Borror, 1979; 57, from Borror & Wicklow, 1983). **56, 57** Infraciliature in ventral view, protargol impregnation and nigrosin-butanol staining, 270 µm, 175 µm. Right from Fig. 56 a middle morphogenetic stage.

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A new genus and species of freshwater crab from Cameroon, West Africa (Crustacea, Brachyura, Potamoidea, Potamonautidae)

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Synopsis. A new species of freshwater crab from Cameroon, West Africa, is described from specimens held in the Natural History Museum (NHM), London, U.K. and in the Museum für Naturkunde der Humboldt-Universitat zu Berlin (MNHU), Germany. After comparison with other genera of freshwater crabs occurring in West Africa the new species was found to represent a new genus.

INTRODUCTION

The present report was prompted by the acquisition of a new freshwater crab specimen from Cameroon by the NHM. The crab was donated in 1987 by Mr David Zeitlin, a Cambridge anthropologist carrying out field work in Cameroon. The specimen was a mature male and proved difficult to identify because its mandibles, gonopods, carapace, and third maxillipeds represented an unusual combination of these important taxonomic characters.

The structure of the mandibles of the specimen placed it in the superfamily Potamoidea Ortmann, 1896 and the family Potamonautidae Bott, 1970, rather than in the Gecarcinucoidea Rathbun, 1904. However, the combination of characters of the third maxillipeds, carapace, and gonopods of this specimen argued against its inclusion in any of the three freshwater crab genera known from West Africa; *Sudanonautes* Bott 1955, *Liberonautes* Bott 1955 and *Potamonautes* Macleay 1838 (Bott, 1955). The specimen was sent to Dr M. Türkay of the Senckenberg Museum for further comment and discussion.

In 1989 one of the authors (NC) examined Zeitlin's freshwater crab from Cameroon during a visit to the Senckenberg Museum, but was unable to identify the specimen at that time. In 1991, several other similar specimens, also from Cameroon, were discovered by one of the authors (NC) while making an examination of the collection of freshwater crabs held in the MNHU. The present report arises out of a subsequent reexamination of Zeitlin's specimen from Cameroon during a visit to the NHM. The material in the NMH and the MNHU is described here as a new species belonging to a new genus.

The following abbreviations have been used: CW = carapace width at widest point; CL = carapace length, measured along median line; CT = cephalothorax thickness, maximum depth of cephalothorax; FW = front width, width of front measured along anterior margin.

SYSTEMATIC ACCOUNT

Potamonemus gen. n.

Diagnosis. No flagellum on exopod of third maxilliped. Mandibular palp two-segmented with a single, undivided,

Table 1 *Potamonemus mambilorum* sp. n. from Cameroon, West Africa. Carapace dimensions and proportions relative to the carapace width of all 16 known specimens. (CW = carapace width; CL = carapace length; CT = carapace thickness; FW = front width; n = 16. Measurements of CW, CL, CT and FW in millimetres).

	CW	CL	CT	FW	CL/CW	CT/CW	FW/CW
NHM—1991: 183, Holotype							
1. ♂	34.5	25.5	12.5	11.5	0.74	0.36	0.33
MNHU—13498 Bambulae, Paratype							
2. ♂	28.5	20.0	10.3	9.2	0.70	0.36	0.32
MNHU—13593 Fsou Grassland, Paratypes							
3. ♂	36.9	25.3	12.1	12.1	0.67	0.33	0.33
4. ♂	33.9	24.6	11.6	11.0	0.73	0.34	0.32
5. ♀	31.1	22.1	10.2	10.2	0.71	0.33	0.33
6. ♀	23.7	16.5	7.3	7.3	0.70	0.31	0.31
MNHU—14141 Yaounde, Paratype							
7. ♀	24.6	17.8	8.6	8.3	0.72	0.35	0.34
MNHU—20162 Bamenda, Paratype							
8. ♂	35.5	24.9	11.6	10.7	0.70	0.33	0.30
MNHU—20183 Bamenda, Paratype							
9. ♀	29.9	21.0	11.7	9.9	0.70	0.39	0.33
10. ♀	20.3	15.1	7.0	7.0	0.74	0.34	0.34
MNHU—20201, Paratype							
11. ♂	35.4	24.5	12.0	11.2	0.69	0.34	0.32
MNHU—20203 Douala, Paratypes							
12. ♂	38.1	27.1	12.4	12.1	0.71	0.33	0.32
13. ♂	30.9	22.0	10.2	10.1	0.71	0.33	0.33
14. ♀	37.8	27.1	11.7	11.3	0.72	0.31	0.30
15. ♀	30.5	21.9	10.5	10.0	0.72	0.34	0.33
16. ♀	28.4	20.4	9.5	9.2	0.72	0.33	0.32

Table 2 *Potamonemus mambilorum* sp. n. length of the legs of the type from Cameroon (CW = 34.5 mm). P1–P5 = pereiopods 1–5; 1 = length of segment; Total Leg Length = sum of length of all five segments; Proportion Total/CW = ratio of total leg length to carapace width.

Leg No.	P1	P2	P3	P4	P5
Segment					
Ishium	4.0	4.0	4.0	4.0	3.0
Merus	12.0	12.0	16.0	16.0	12.5
Carpus	17.0	7.0	8.0	8.0	8.0
Propodus	37.0	8.0	7.0	8.0	7.0
Dactylus	26.0	10.0	10.0	11.0	8.0
Total Leg Length (mm)	96.0	41.0	45.0	47.0	38.5
Proportion Total/CW	2.78	1.19	1.30	1.36	1.12

end segment. End segment of gonopod 2 very short (one tenth the length of the penultimate segment); end segment of gonopod 1 curving outwards away from the medial line when viewed from the lateral aspect; end segment of gonopod 1 with a longitudinal groove on posterior aspect. Second sternal groove incomplete, reduced to two short notches at the lateral edges of the sternum at the bases of the chelipeds.

HOLOTYPE. NHM reg. 1991:183, from Somié Village, Tikow Plain, Cameroon (6°30′N, 11°30′E), 760 metres. Collected by David Zeitlin.

Potamonemus mambilorum sp. n.
(Figs 1–3, Tabs 1–2, pl. 1a, b)

Potamonautes anchetiae; Balss 1929:117 (part).
Potamonautes (Isopotamonautes) anchetiae; Bott 1955:247 (part).

DIAGNOSIS. Major (right) cheliped of male enlarged, longer and higher than left (minor) cheliped, dactylus of cheliped arched forming permanent gape between the fingers when the chelipeds are closed; end segment of gonopod 1 with curving longitudinal groove on posterior surface; exorbital and epibranchial teeth small and low; vertical flank groove meeting anterolateral margin at the base of the epibranchial tooth; carapace smooth, no deep grooves.

DISTRIBUTION. The forested highlands of southwest Cameroon (Bamenda, Bambulae, Fsou Grasslands), and the forested lowlands of south Cameroon (Douala, Yaounde).

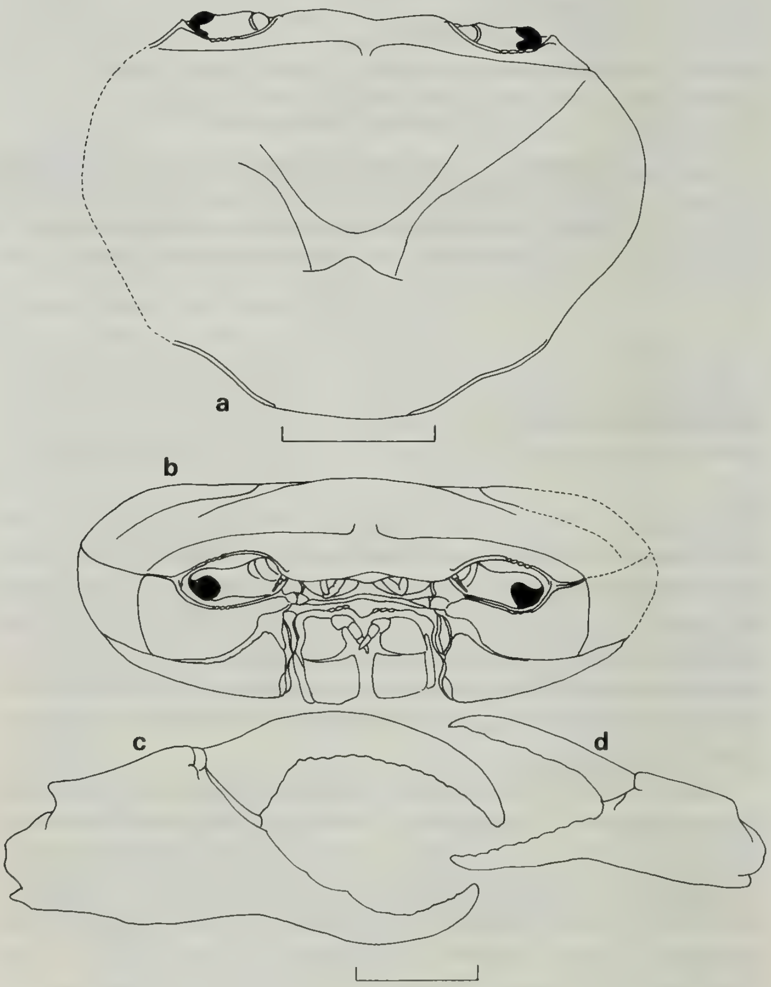

Fig. 1 *Potamonemus mambilorum* sp. n., from Tikow Plain, Cameroon, male, type, carapace width = 34.5 mm. a, cephalothorax, dorsal aspect; b, cephalothorax, frontal aspect; c, right cheliped, lateral aspect; d, left cheliped, lateral aspect. Scale bars equal 10.0 mm.

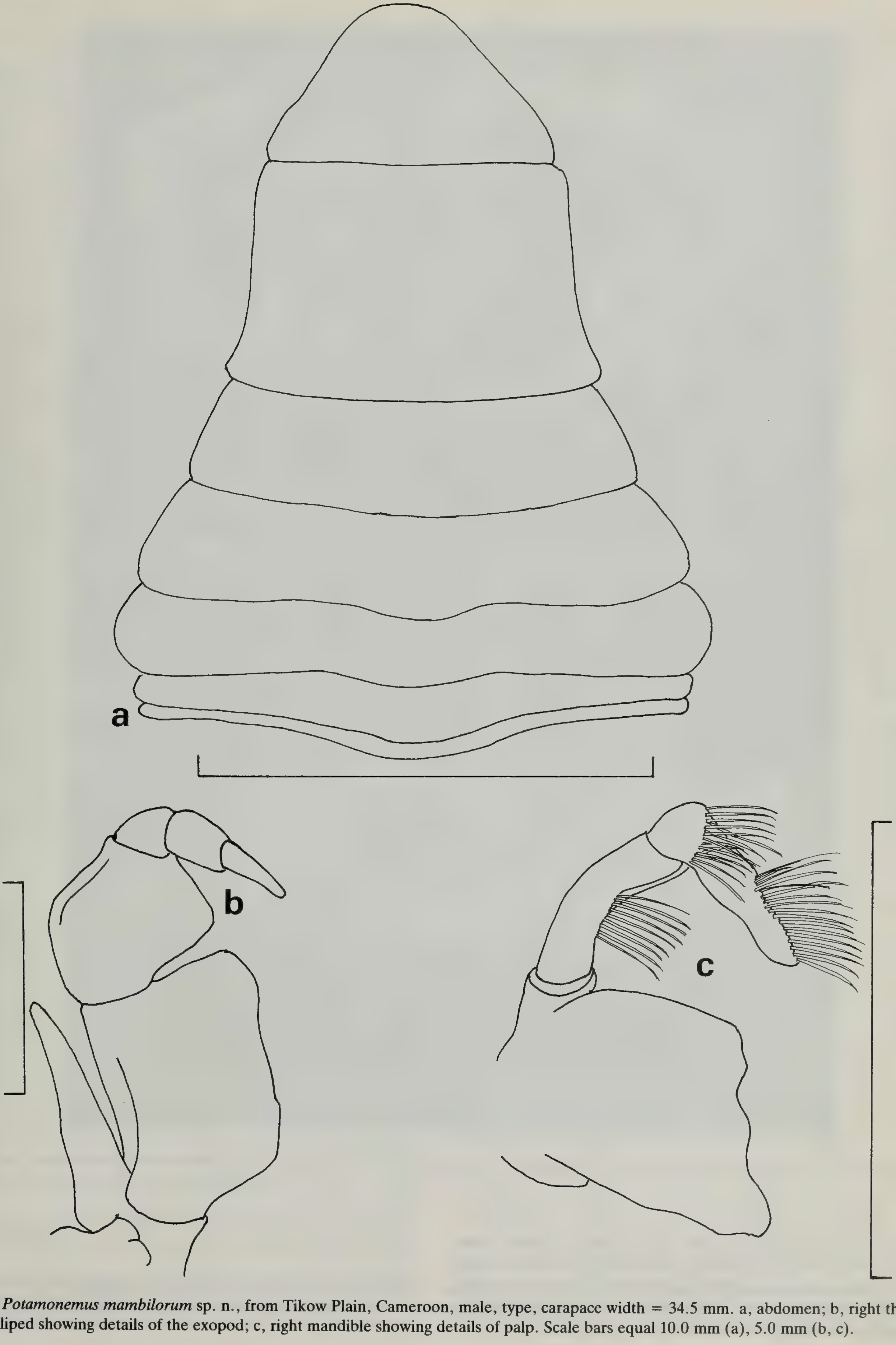

Fig. 2 *Potamonemus mambilorum* sp. n., from Tikow Plain, Cameroon, male, type, carapace width = 34.5 mm. a, abdomen; b, right third maxilliped showing details of the exopod; c, right mandible showing details of palp. Scale bars equal 10.0 mm (a), 5.0 mm (b, c).

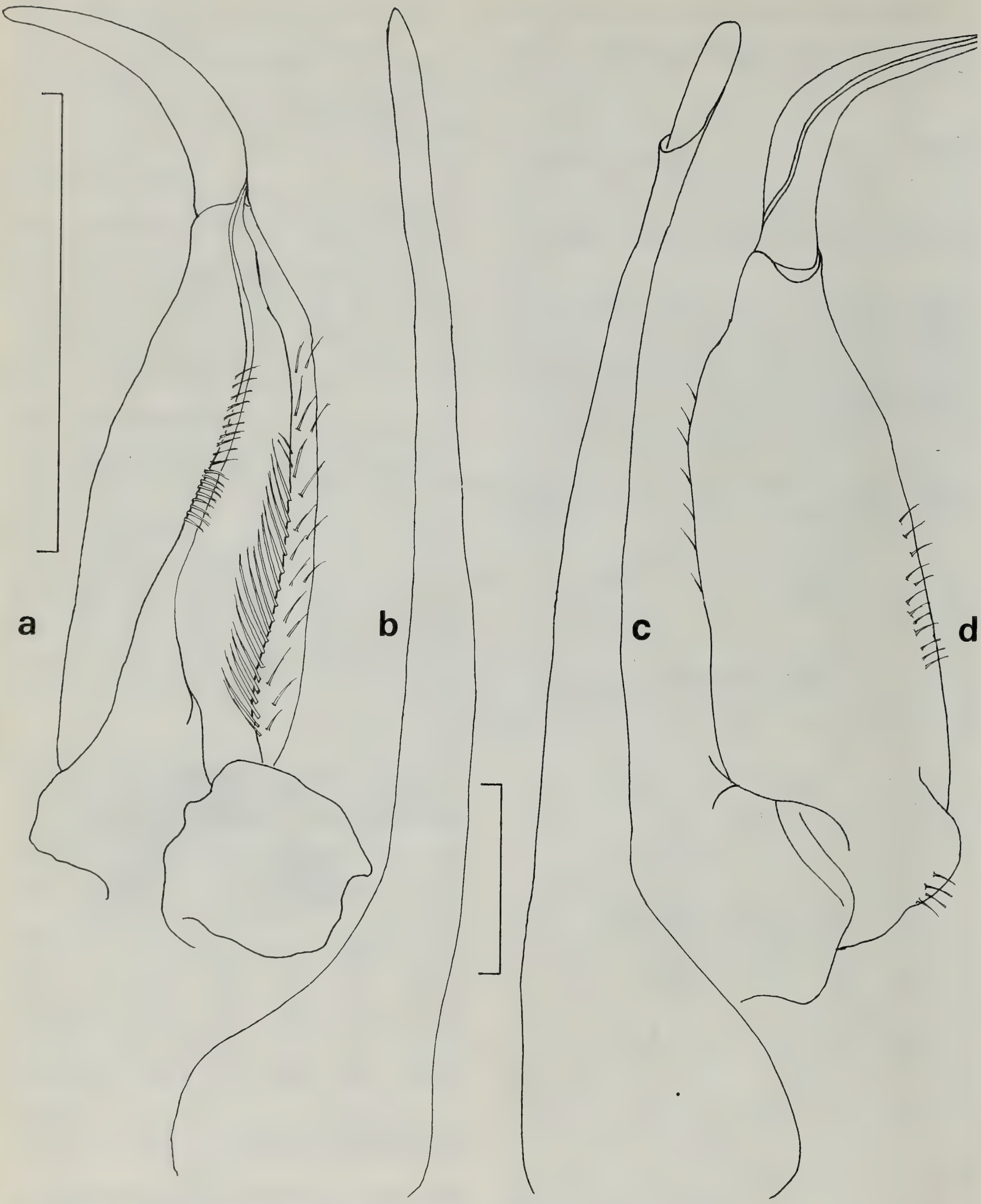

Fig. 3 *Potamonemus mambilorum* sp. n., from Tikow Plain, Cameroon, male, type, carapace width = 34.5 mm. a, right gonopod 1, ventral aspect; b, right gonopod 2, ventral aspect; c, right gonopod 2, dorsal aspect; d, right gonopod 1, dorsal aspect showing groove. Scale bars equal 5.0 mm (a,d), 1.0 mm (b,c).

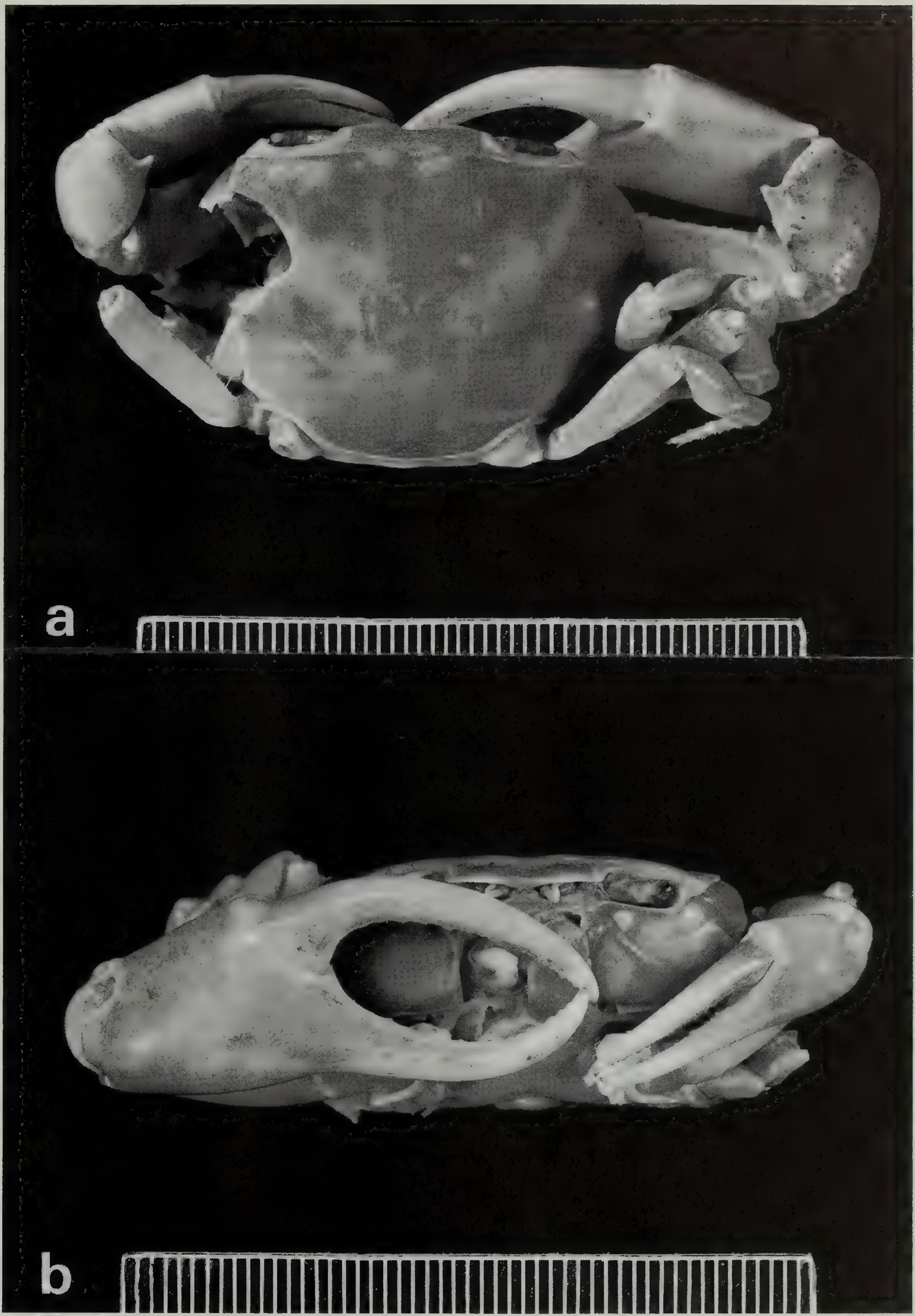

Plate 1.a, *Potamonemus mambilorum* sp. n. Dorsal view, scale bar in mm; b, *Potamonemus mambilorum* sp. n. Frontal view, scale bar in mm. Photos by Phil Crabb, NHM Photo Unit.

MATERIAL

Holotype. NHM reg. 1991:183. Paratypes: Fifteen additional specimens of *P. mambilorum* are held in the MNHU. All re-identified by one of the authors (NC). This material was formerly identified as *Potamonautes anchetiae* Brito-Capello 1871 by Dr H. Balss. MNHU-13498, from Bambulae near Bamenda, Cameroon, Collected by Oberl. Ader, 2/IV/1909, 1m; MNHU-13593, from Fsou Grassland 1100m, Cameroon, Collected by Oberl. Bartsch, 2m, 2f; MNHU-

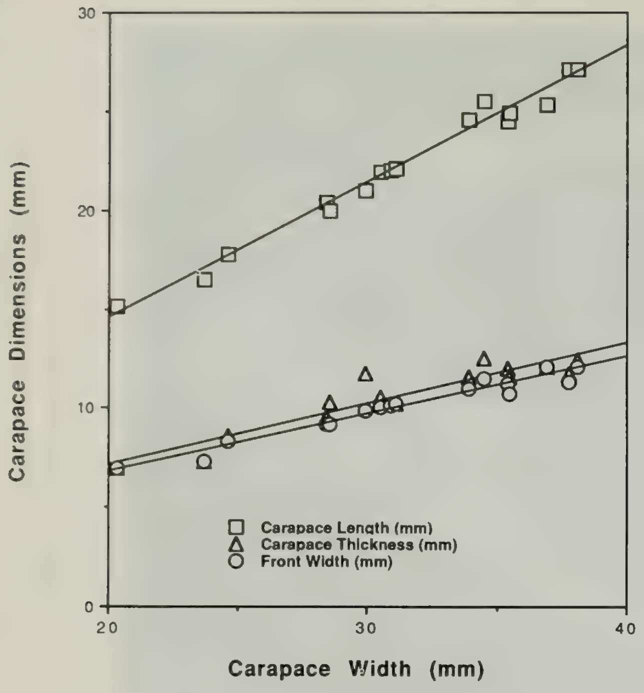

Fig. 4 Comparisons of 16 specimens of *Potamonemus mambilorum* sp. n. ranging in size from CW = 20.30 mm to 37.8 mm, all from Cameroon. Dimensions of the carapace (CL, CT, FW) compared to body size (CW). Relationships are described by the following regression equations: $CL = 0.77 + 0.619\,CW$, $r = 0.99$; $CT = 0.97 + 0.31\,CW$, $r = 0.933$; $FW = 1.06 + 0.29\,CW$, $r = 0.975$. All r values indicate a highly significant correlation ($P < 0.001$), at 14 degrees of freedom. CW = carapace width at the widest point; CL = carapace length, measured along the median line; CT = cephalothorax thickness, the maximum depth of the cephalothorax; FW = front width, the width of the front measured along the anterior margin; r - correlation coefficient.

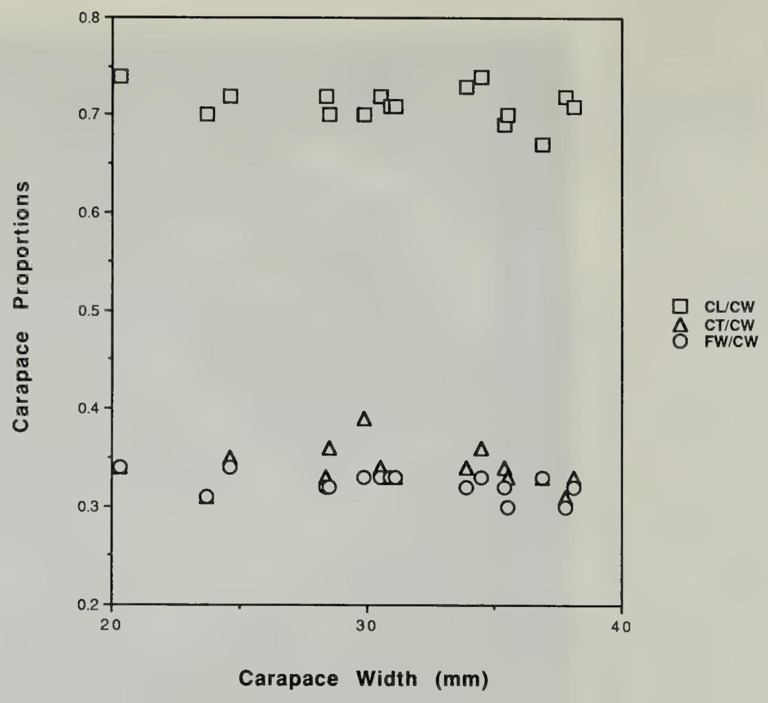

Fig. 5 Comparisons of 16 specimens of *Potamonemus mambilorum* sp. n. ranging in size from CW = 20.30 mm to 37.8 mm, all from Cameroon. Relative proportions of the carapace (CL/CW, CT/CW, and FW/CW) compared to body size (CW). The relationships are described by the following regression equations: $CL/CW = 0.745 - 0.001\,CW$, $r = 0.313$; $CT/CW = 0.356 - 0.001\,CW$, $r = 0.148$; $FW/CW = 0.356 - 0.001\,CW$, $r = 0.456$. The r values for CL/CW, CT/CW, and FW/CW indicate no significant correlation ($P > 0.05$), at 14 degrees of freedom. CW = carapace width at the widest point; CL = carapace length, measured along the median line; CT = cephalothorax thickness, the maximum depth of the cephalothorax; FW = front width, the width of the front measured along the anterior margin; r = correlation coefficient.

14141, from Yaounde station, south Cameroon, Collected by Oberl. v. Somerfeld, 1f; MNHU-20162, from Bamenda, Cameroon. Collected by Adametz and Naumann, 12/XI/1909, 1m; MNHU-20183, from Bamenda, Cameroon. Collected by Lt Naumann, 15/I/1912, 2f; MNHU-20201, from Cameroon. Collected by Weibel, 1m; MNHU-20203, from Douala, Cameroon. Collected by Thorbecke, 29/X/1912, 2m, 3f.

DESCRIPTION

The following description is based on the male holotype (NHM reg. 1991:183, CW = 34.5 mm).

CARAPACE (Figs 1a,b; Tab. 1; pl. 1a,b). The cephalothorax is ovoid, widest at the anterior third (ratio of CL to CW = 0.36) and distinctly arched, with the maximum depth in the anterior region (ratio of CT to CW = 0.74). The anterior margin of the front is straight and wide, one-third the width of the carapace (ratio of FW to CW = 0.33). The carapace texture is smooth, no granules are visible, even under magnification, and there are no deep grooves; the cervical and semi-circular grooves are faint. The exorbital tooth is blunt and low and the epibranchial tooth is almost undetectable. There is no detectable intermediate tooth on the anterolateral magin between the exorbital and epibranchial teeth. The anterolateral margin is smooth (lacking teeth, spines, or granulations) behind the epibranchial tooth, and this margin is smoothly continuous with the posterior margin. The anterolateral margins do not curve inward over the surface of the carapace in the branchial regions. The postfrontal crest extends laterally across the entire carapace, meeting both anterolateral margins at the epibranchial teeth; there is a short groove at the mid point of the postfrontal crest.

Each flank has a long longitudinal groove dividing the subhepatic region from the pterygostomial region, and a shorter vertical groove in the subhepatic region beginning at the longitudinal groove and ending at the anterolateral margin at the base of the epibranchial tooth. These two grooves divide the flanks into three parts. The first sternal groove is complete, and the second sternal groove is reduced to two small notches at the sides of the sternum. The third maxillipeds fill the entire oral field, except for the efferent openings, which are oval. There is no flagellum on the exopod of the third maxilliped (Fig. 2b). The mandibular palp is two-segmented with a single, undivided, end segment (Fig. 2c). The first five segments of the male abdomen are broad but short and taper inward; the last two segments are long and narrow (A6, A7), the last segment (A7) is rounded at the distal margin (Fig. 2a). A small to medium-sized species, mature at CW = 29.0 mm.

GONOPODS (Figs 3a,d). The end segment of gonopod 1 is long, (half as long as penultimate segment), lacking a longitudinal groove on the anterior surface, but with a twisting longitudinal groove visible on the posterior surface, running from the junction with the penultimate segment to the tip of the end segment. The end segment of gonopod 1 curves outwards away from the medial line when viewed from the lateral aspect, is widest at the half way point, and ends in a pointed tip. The distal region of the penultimate segment of gonopod 1 is slim, tapering to the junction with the end segment. Gonopod 2 is shorter than gonopod 1 (reaching only the junction between the segments of gonopod 1). The end segment of gonopod 2 is extremely short, only one-tenth as long as the penultimate segment. The end segment of gonopod 2 is not solid, its sides are thin and folded inward enclosing an inward-facing hollow; the tip is rounded. The penultimate segment of gonopod 2 is widest at its base, tapering sharply inward about one-third along its length, the last two-thirds form a long, thin, tapering, upright process which supports the end segment.

CHELIPEDS (Figs 1c,d; pl. 1b). The chelipeds of the male are markedly unequal, the right is much longer (37.0 mm) and higher (14.5 mm) than the left (26.5 mm and 8.5 mm respectively). The length of the ventral margin of the propodus of the right cheliped alone (37.0 mm) is greater than the width of the carapace at its widest point (34.5 mm). The palm of the right dactylus is swollen, the fingers gape widely when closed; the ends of the dactylus and pollex end in sharp, overlapping points (pollex over dactylus). The left cheliped is small, and lacks the arched dactylus and swollen palmar region; its dactylus and pollex touch along the entire length when closed except for a small gap in the proximal region. The pereiopods are slender and the proportions of the various segments are given in Table 2; P4 is the longest leg, P5 the shortest leg; the dactylus of P5 is very short.

GROWTH. The dimensions of the carapace (CL, CT and FW) of *P. mambilorum* increase with increasing body size (CW) in the manner described in Fig. 4. The carapace thickness was found to be almost equal to the front width over the range of sizes from CW = 20.3 mm to CW = 38.1 mm. These dimensions are expressed as a ratio of the carapace width in Fig. 5, which indicates that the relative proportions of the carapace (CL/CW, CT/CW and FW/CW) do not alter with increasing body size. The r values of 0.313, 0.148 and 0.456 respectively showed no significant correlation ($P > 0.05$, d.f. = 14) over a range of sizes, indicating that larger crabs have proportionally the same sized carapaces as smaller specimens (Fig. 5).

ECOLOGICAL NOTES

The collector of the type specimen provided the following comments on the crab. *Potamonemus mambilorum* is a riverine crab and is eaten by the Mambila tribe especially during the dry season, when crabs are caught by bailing out drying sections of river beds. The Mambila people call this species the ‘Kap’ crab. A second species of freshwater crab is sympatric with *P. mambilorum* and was identified as *Sudanonautes faradjensis* (Rathbun, 1921). The local name for this species is the ‘Nyar’ crab.

TAXONOMIC REMARKS

Not all of the material assigned by Balss (1929) to *Potamonautes anchetiae* Brito-Capello 1871 was examined because the MNHU only has 15 specimens of the original Cameroon collection. It is these that are redescribed here as *Potamonemus mambilorum*. Bott (1955) has referred the MNHU material identified by Balss to *Potamonautes (Isopotamonautes) anchetiae* together with additional specimens collected from Zaire. However the specimens from Zaire and Cameroon differ. For example, the specimens from Zaire possess two deep sternal grooves, the anterolateral margin of the carapace curves inward over the surface of the carapace in the branchial region, and they have a thread-shaped end segment on gonopod two. In contrast, in the specimens from Cameroon only the first sternal groove is deep and clear, the second is absent except for two side notches, the anterolateral margin is continuous with the posterolateral margin, and the end segment of gonopod 2 is very short indeed.

Potamonemus mambilorum has a two-segmented mandibular palp, with a single (simple) end segment, which places it in the superfamily Potamoidea and the family Potamonautidae, rather than in the Gecarcinucoidea. This new species could not be assigned to any genera of the Potamonautidae (*Potamonautes, Sudanonautes* and *Liberonautes*) for the following reasons. *Potamonautes* and *Liberonautes* are characterised by a long thread-like end segment of gonopod 2. The short end segment of gonopod 2 of *P. mambilorum* prevents the inclusion of this species in *Potamonautes* and *Liberonautes* (Bott, 1955; Cumberlidge, 1985; Cumberlidge and Sachs, 1989a,b). The very short end segment of gonopod 2 is a characteristic of *Sudanonautes*. However, the Cameroon material cannot be assigned to *Sudanonautes* since all specimens lack a flagellum on the exopod of the third maxilliped, a character considered here and elsewhere to be of taxonomic significance at the genus level and above (Bott, 1959, 1969, 1970; Cumberlidge, 1987). In addition, *P. mambilorum* lacks an intermediate tooth, the presence of which is another characteristic of *Sudanonautes*. These features justify the recognition of a new genus.

ETYMOLOGY. The new genus has been named *Potamonemus* to recognise the distribution of the species in a tropical rain forest habitat. The species is restricted to a forested highland area of southwest Cameroon and a forested lowland area in south Cameroon. These areas are included within the boundaries of one of Africa’s Pleistocene forest refuges (Kingdon, 1989). *Potamonemus* (Neuter) from the Greek; Potamo a contraction of the family name and nemos meaning forest. The species has been named for the Mambila people of Cameroon who know *Potamonemus mambilorum* well, and use this species as a seasonal food source.

ACKNOWLEDGEMENTS. We should like to thank Mr David Zeitlin of Cambridge University, Cambridge, U.K. for bringing the material to our attention. We should also like to acknowledge the contributions of Prof H.-E. Gruner of the Zoologisches Museum, Museum für Naturkunde der Humboldt-Universitat zu Berlin, Germany, Dr M. Türkay, of the Senckenberg Museum, Frankfurt, Germany and Phil Crabb (NHM Photo Unit) for the photographs reproduced in this paper. Part of this work (NC) was supported by a Faculty Grant from Northern Michigan University, Marquette, Michigan, USA.

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On the discovery of the male of *Mormonilla* Giesbrecht, 1891 (Copepoda: Mormonilloida)

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SYNOPSIS. Males of the two known species of *Mormonilla* Giesbrecht are described in detail for the first time. They have reduced or vestigial mouthparts and are probably non-feeding. Males have a single testis and produce a single spermatophore. Male antennules are geniculate. A system of probable segmental homologies for the antennulary segments is proposed and the supporting evidence for this system discussed. Females carrying egg sacs are reported and figured for the first time. *Mormonilla* is unusual amongst copepods in producing paired egg sacs from a common medial genital aperture.

INTRODUCTION

The order Mormonilloida was established by Boxshall in 1979 to accommodate the family Mormonillidae which consists of a single genus, *Mormonilla*, containing two species, *M.phasma* Giesbrecht, 1891 and *M.minor* Giesbrecht, 1891 (Boxshall, 1979). Both species have a very widespread distribution in the midwater oceanic plankton, especially at depths between 400 and 1000m. The skeletomusculature and external morphology of the feeding apparatus of adult females of *Mormonilla* indicate that they are small particle feeders (Boxshall, 1985). In a brief review of their biology Boxshall (1986) noted that no males of *Mormonilla*, or females carrying egg sacs have ever been reported, although he had observed a single female with a spermatophore attached to its median genital aperture.

Mormonilla is relatively common in the Arabian Sea, in the deep eastern Indian Ocean, and in the Gulf of Aden; in the Red Sea its occurrence is restricted to the southernmost parts only (Beckmann, 1984; Böttger-Schnack, unpubl.). In zooplankton samples collected using a very fine mesh net (0.055 mm) several males were found, in addition to numerous females bearing egg sacs or spermatophores and some copepodid stages. The males of both species are described below in detail and short notes are presented on the reproductive biology of the genus.

MATERIALS AND METHODS

The specimens of *Mormonilla* were collected during cruises of the German Research Vessel *Meteor* using a multiple opening-closing net (Weikert & John, 1981) of mesh size 0.055 mm hauled vertically. The majority of the material was taken in the Arabian Sea and in the Strait of Bab el Mandab, the southern entrance of the Red Sea, during *Meteor* cruise 5/3a+b and 5/5 respectively (see Table 1). A single ovigerous

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Table 1. *Mormonilla* specimens from the Arabian Sea, the Red Sea, the Mediterranean Sea and the eastern Indian Ocean.

Station	Position	Date	Depth	Number of specimens
Arabian Sea				
347	20°44′N 59°40′E	5.4.87	1250–1450m	1 ♀ *M.phasma* (ovigerous) 2 ♂ *M.phasma*
347	″	5.4.87	1450–1650m	42 ♀ *M.phasma* (2 ovigerous) 1 ♀ *M.phasma* (+ spermatophore) 1 ♂ *M.phasma* 57 copepodid stages 34 ♀ *M.minor* (2 ovigerous)
347	″	5.4.87	1650–1850m	1 ♀ *M.phasma* (ovigerous) 1 ♀ *M.minor* (+ spermatophore)
496	18°00′N 66°25′E	12.5.87	1650–1850m	2 ♀ *M.phasma* (ovigerous) 1 ♀ *M.phasma* (+ spermatophore) 2 ♀ *M.minor* (ovigerous)
Bab el Mandab, Red Sea				
717	12°2′N 43°24.5′E	6.8.87	125–150m	7 ♂ *M.minor*
Eastern Mediterranean Sea				
34/35	34°25′N 26°14′E	20.1.87	100–150m	2 ♀ *M.minor* 1 ♂ *M.minor* 2 copepodid stages
34/35	34°25′N 26°4′E	20.1.87	600–750m	1 ♀ *M.minor* (ovigerous) 1 ♂ *M.minor*
Eastern Indian Ocean				
11	04°47′S 87°14′E	24.1.77	200m	1 ♂ *M.minor*
11	″	24.1.77	600m	2 ♂ *M.phasma*
11	″	24.1.77	800m	2 ♂ *M.phasma*
11	″	24.1.77	1000m	2 ♂ *M.phasma*

female of *M.phasma* was also found in zooplankton samples collected during *Meteor* cruise 64 at a depth of 550–650 m in the upwelling area of the N.W. African coast in spring of 1983 using a multiple opening-closing net of 0.3 mm mesh size.

The specimens were dissected in lactic acid and examined as temporary mounts in lactophenol. All drawings were prepared using a camera lucida on a Leitz Dialux 20 interference microscope. All appendage segments and setation elements are named and numbered using the system established by Huys & Boxshall (1991). The material is stored in the collections of The Natural History Museum, London, BM(NH) Reg.Nos. 1992.38–81.

DESCRIPTION OF MALE *Mormonilla phasma*

Body slender, cyclopiform (Fig. 1A–B). Body length of figured specimen 1.42 mm; range 0.90 to 1.42 mm (based on 7 specimens). Prosome 5-segmented, comprising cephalosome and 4 free pedigerous somites; urosome 5-segmented, comprising fifth pedigerous, genital and 3 free abdominal somites. Genital somite with functional genital aperture on left side only. Anal somite about 1.67 times longer than wide; ornamented with patches of fine spinules on ventral surface (Fig. 6A). Rostral region poorly developed, with pair of sensilla (Fig. 2A). Caudal rami elongate, about 18 times longer than wide (Fig. 5C); armed with 6 setae; seta I lacking, seta II located 34% of distance along ramus, setae III to VI postioned around distal margin, seta VII located dorsally, just anterior to rear margin. Ramus ornamented with fine denticles.

Antennule indistinctly 8-segmented (Fig. 2A); with well developed geniculation separating segments 7 and 8. Part proximal to geniculation comprising long proximal segment armed with 1 long and 6 short naked setae and 1 large aesthetasc, a middle section consisting of 5 poorly separated segments bearing 2, 2, 2 + 1 aesthetasc, 2 and 2 elements, and a long distal segment armed with 1 long and 2 short setae and 1 aesthetasc proximally, 2 hirsute setae at midlength (Fig. 2B) and a curved subapical seta. Apical segment slender, bearing 3 subapical setae, one of which with biarticulate base.

Antenna biramous (Fig. 2C) with partly fused coxa and basis, both unarmed. Endopod 2-segmented; proximal segment indistinctly separated from basis, unarmed; distal segment representing fused second and third endopodal segments, armed with 11 setae around apex. Exopod 9-segmented, setal formula 1,0,0,0,0,1,1,1,3. Seta on first exopodal segment plumose, setae on distal part of ramus sparsely spinulate.

Labrum (Fig. 3A) a simple rounded lobe. Paragnaths small, ridge-like lobes.

Mandible (Fig. 4A) biramous; coxal gnathobase extremely reduced with poorly developed blades on margin (Fig. 4B); basis unarmed; endopod 2-segmented, first segment unarmed, second segment with 5 plumose setae; exopod 4-segmented with 2,1,1,2 setal formula (Fig. 4C).

Maxillule biramous (Fig. 3B); praecoxa with weakly developed arthrite (Fig. 3C); coxa and basis fused, bearing single

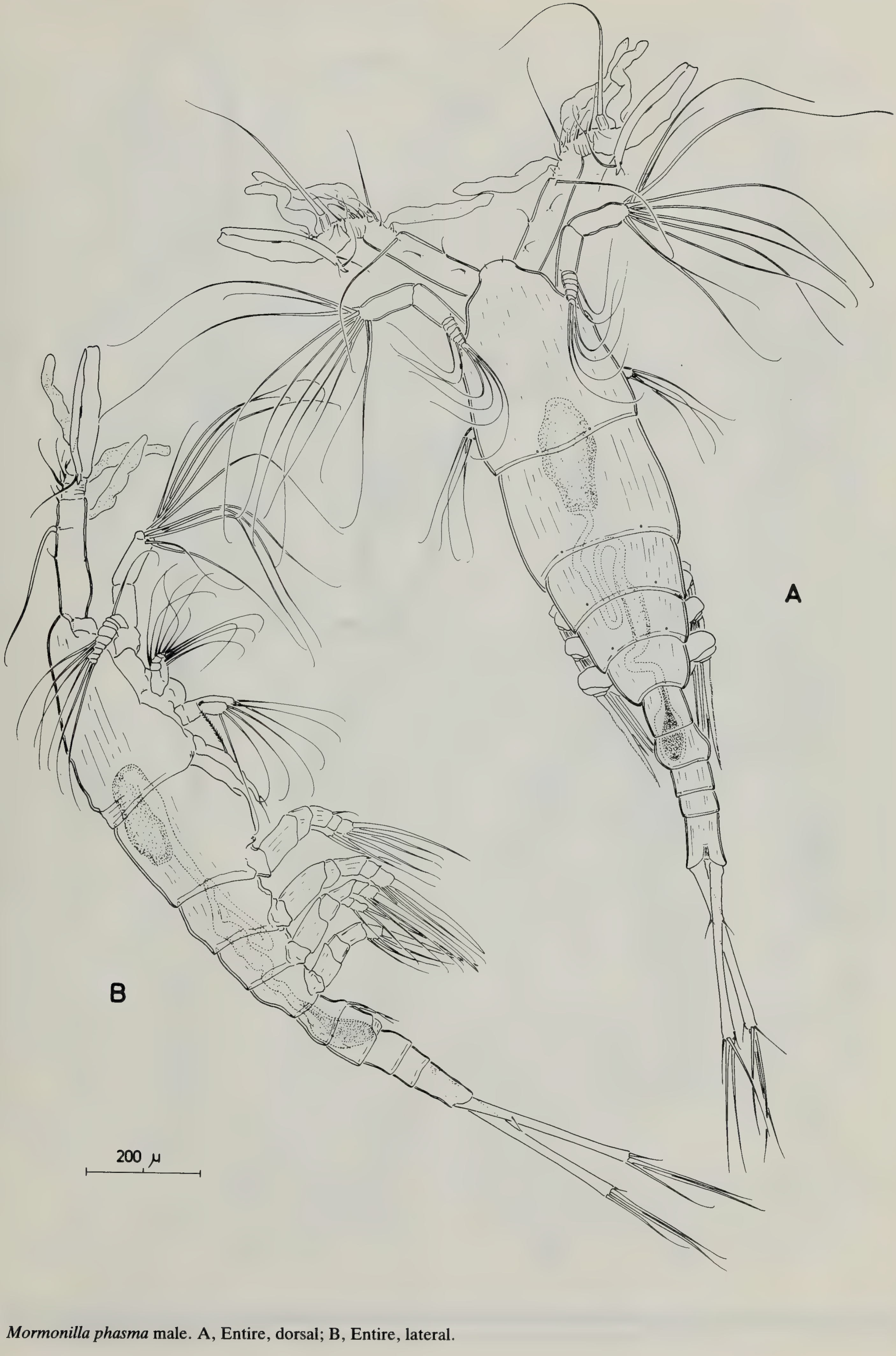


Fig. 1 *Mormonilla phasma* male. A, Entire, dorsal; B, Entire, lateral.

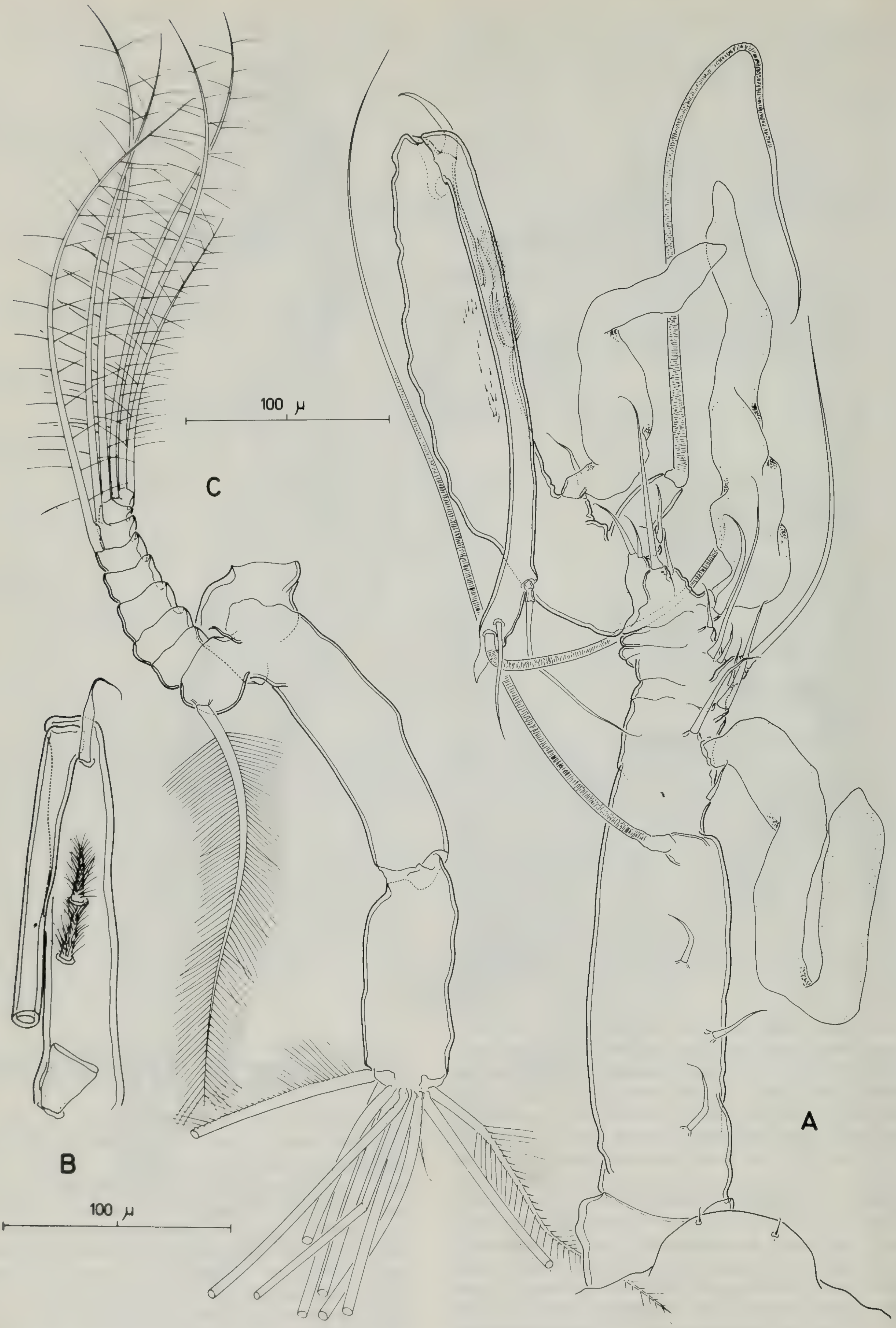


Fig. 2 *Mormonilla phasma* male. A, Antennule, dorsal; B, Detail, showing compound segment proximal to geniculation, anterior; C, Antenna, anterior.

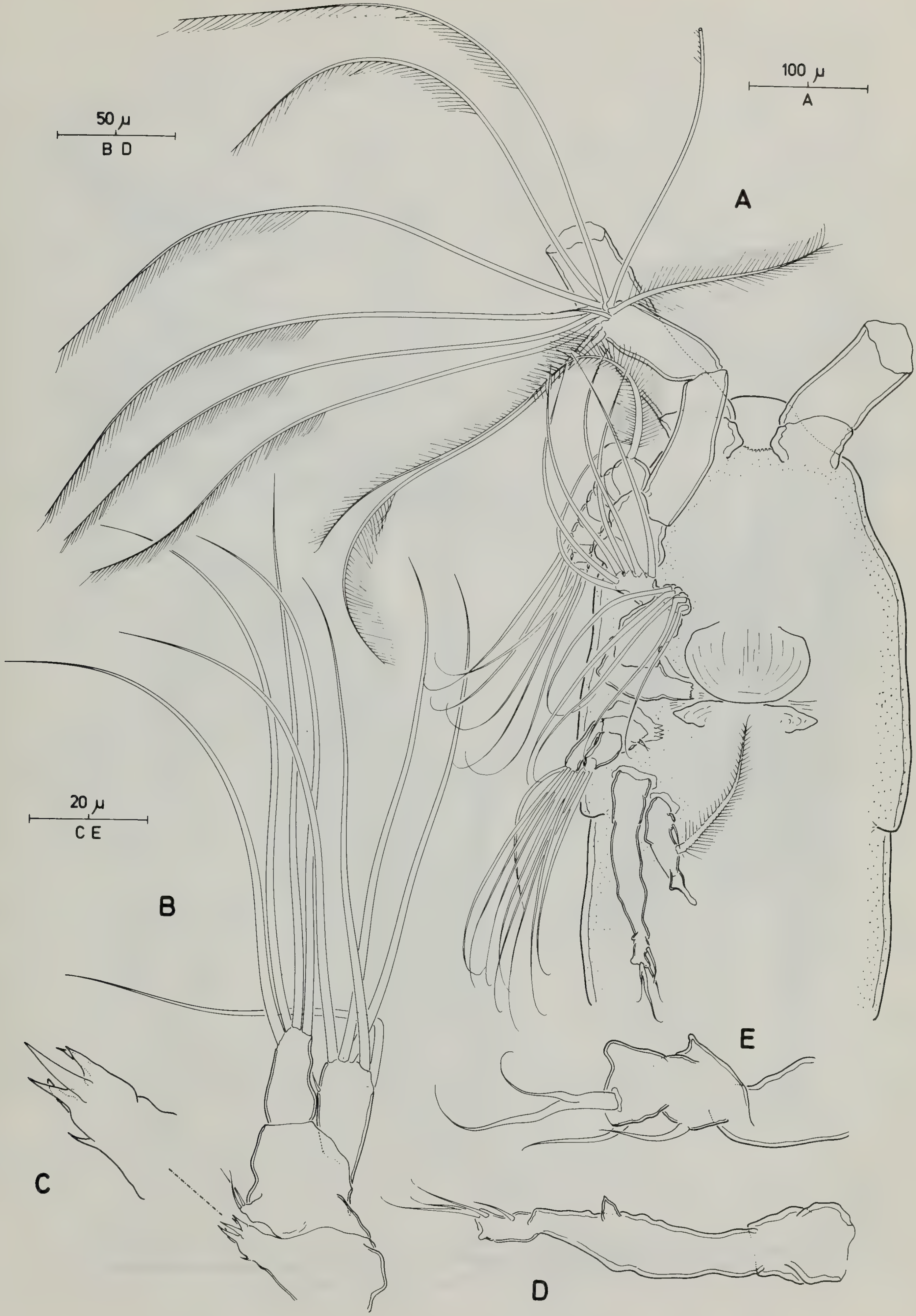
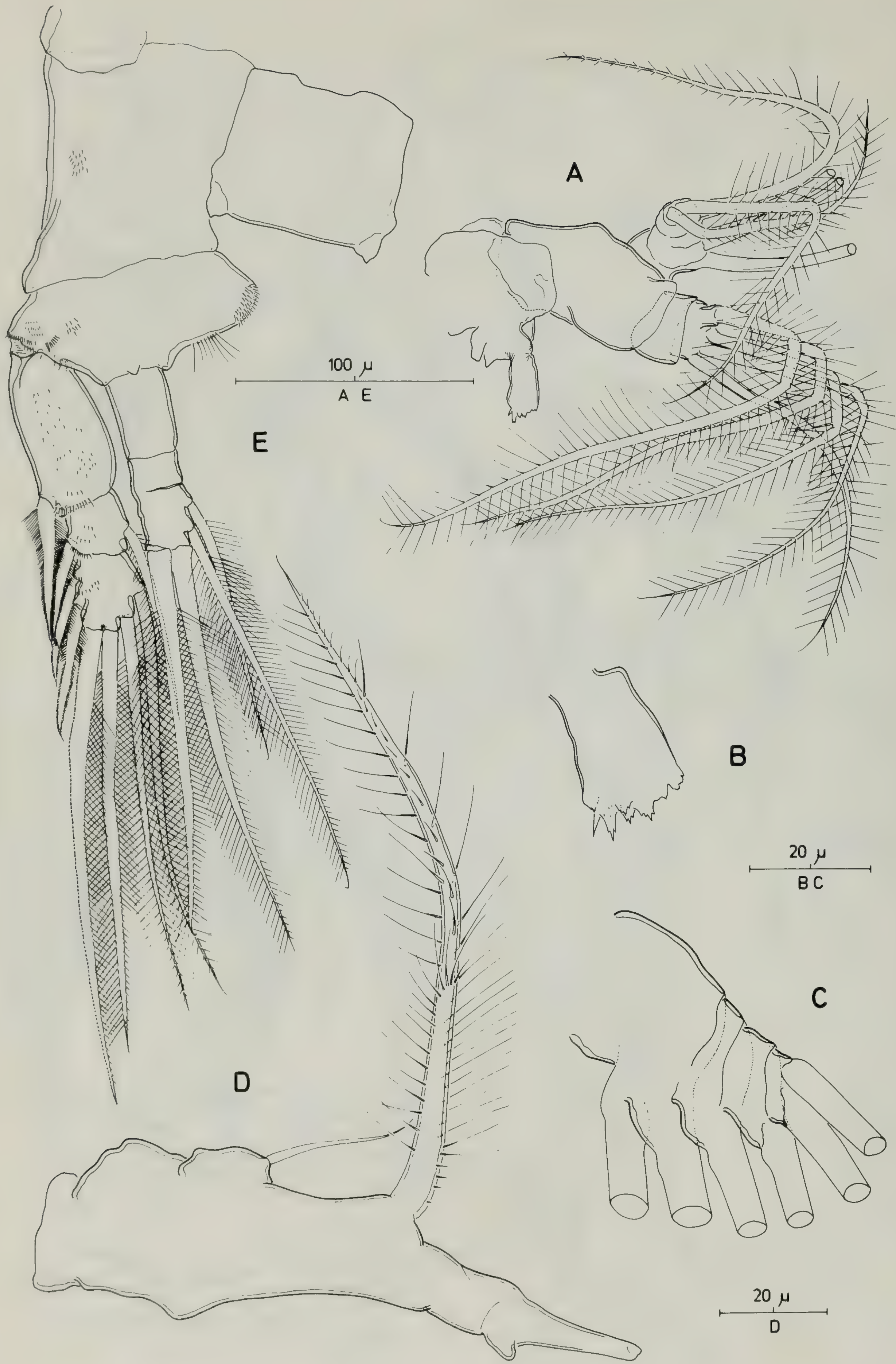


Fig. 3 *Mormonilla phasma* male. A, Cephalosome, ventral view showing cephalosomatic appendages on right side only; B, Maxillule, posterior; C, Detail of praecoxal arthrite of maxillule; D, Maxilla, anterior; E, Maxilla, lateral.


A
100 µ
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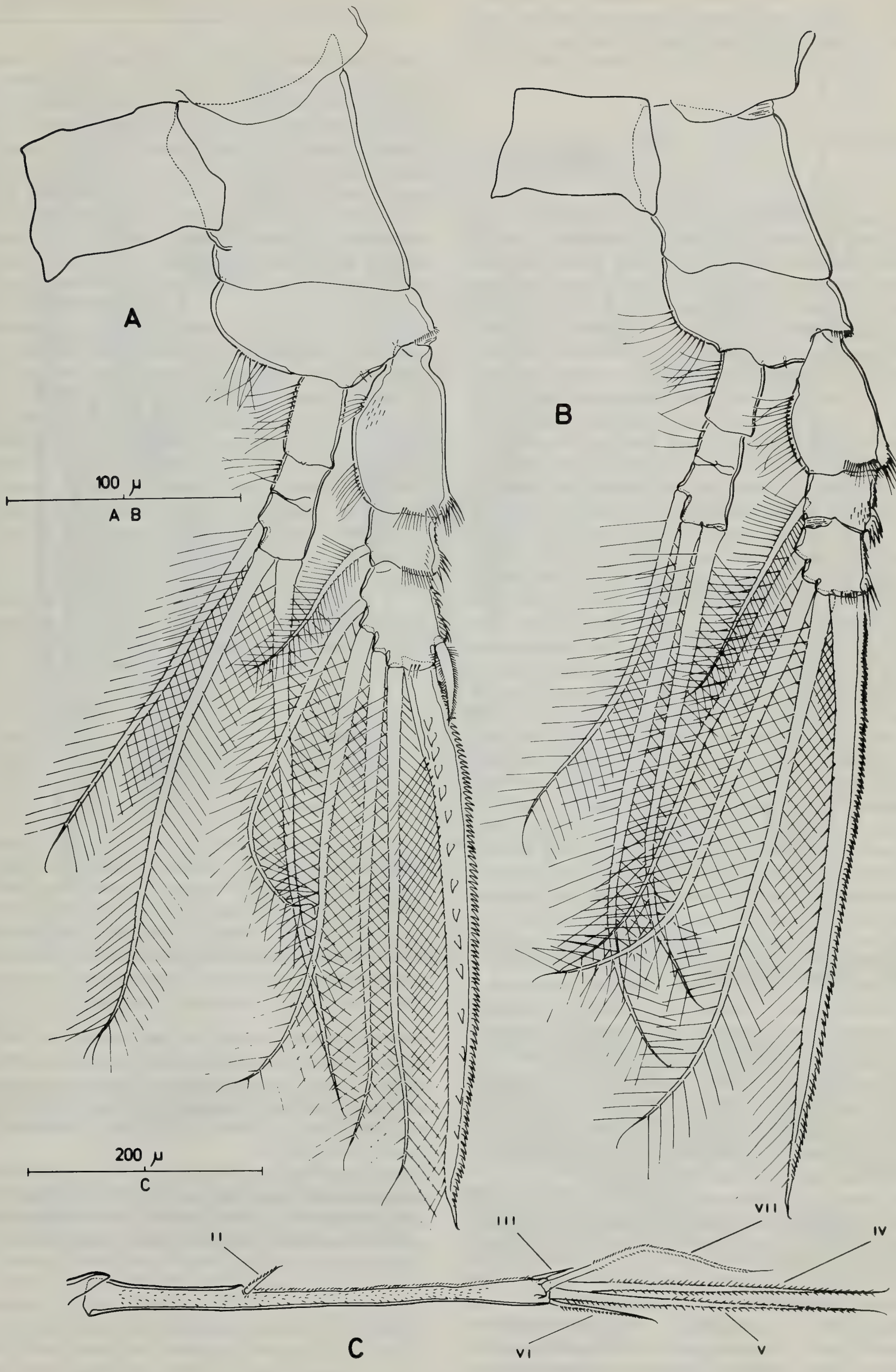
B
20 µ
B C
C
D
20 µ
D

Fig. 4 *Mormonilla phasma* male. A, Mandible, anterior; B, Detail of mandibular gnathobase; C, Detail of mandibular exopod; D, Maxilliped, anterior; E, First leg, anterior.


A
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C
II
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VII
IV
VI
V
C

Fig. 5 *Mormonilla phasma* male. A, Second leg, anterior; B, Third leg, anterior; C, Caudal ramus, dorsal.

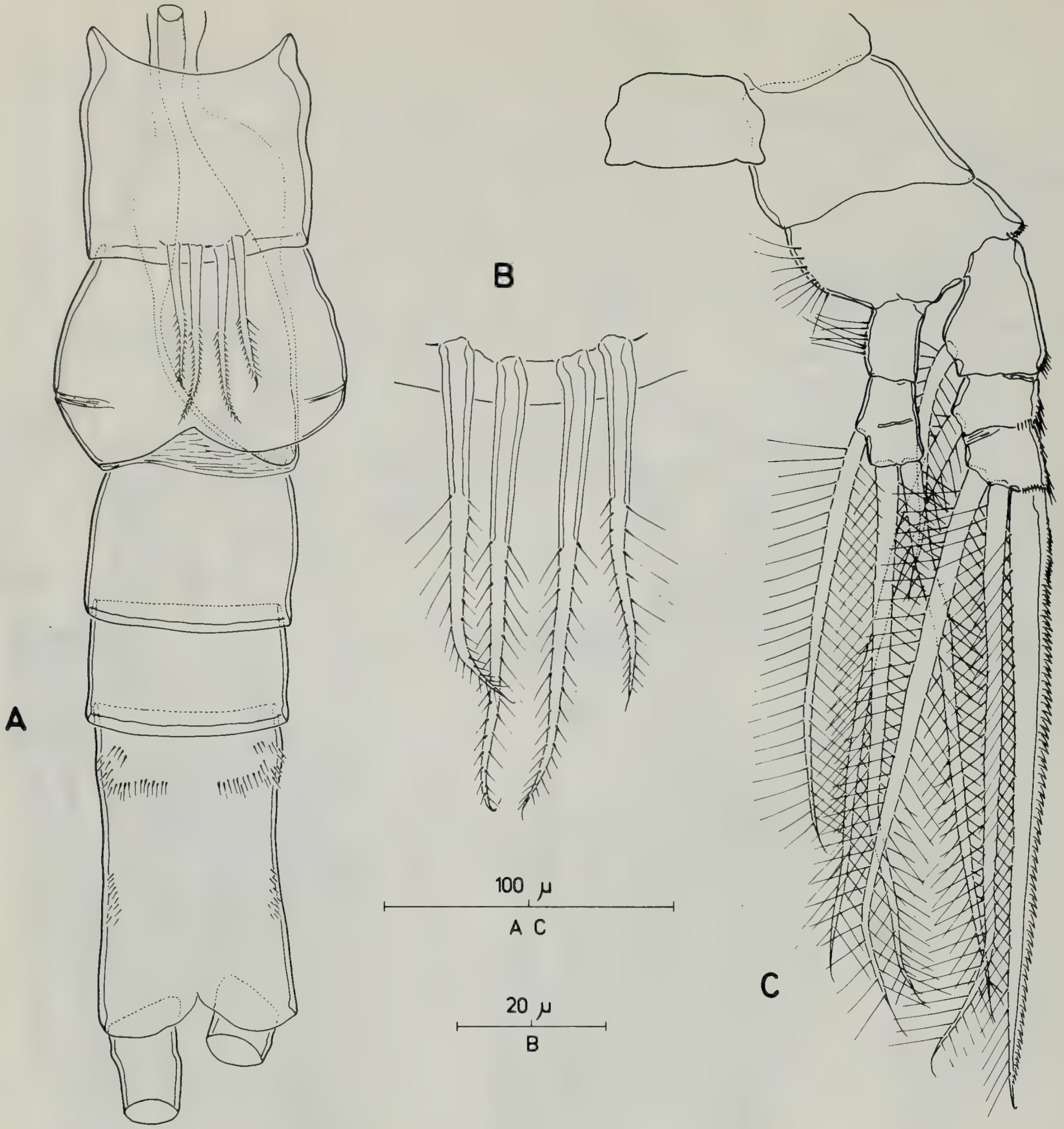

Fig. 6 *Mormonilla phasma* male. A, Urosome, ventral view showing single spermatophore present inside vas deferens on left side; B, Fifth leg, ventral; C, Fourth leg, anterior.

proximal endite with 2 setae; endopod 1-segmented with 4 distal setae; exopod 1-segmented with 5 distal setae.

Maxilla vestigial (Fig. 3D-E); reduced to indistinctly 2-segmented lobe bearing 1 bifid and 2 naked, simple setae distally and a spinous process at midlength. Maxilliped vestigial (Fig. 4D), reduced to unsegmented, tapering lobe bearing a short naked seta and 1 large plumose seta.

Swimming legs 1 to 4 biramous (Figs. 4E, 5A-B, 6C) with 3-segmented exopods and indistinctly 3-segmented endopods. Endopodal segments 2 and 3 partly fused in all legs. Spine and setal formula as follows:

	Coxa	Basis	Exopod	Endopod
Leg 1	0–0	0–0	I–0;I–1;II,I,3	0–0;0–0;0,2,2
Leg 2	0–0	0–0	0–0;0–1;I,I,4	0–0;0–0;0,2,1
Leg 3	0–0	0–0	0–0;0–1;0,I,3	0–0;0–0;0,2,1
Leg 4	0–0	0–0	0–1;0–1;0,I,2	0–0;0–0;0,2,1

Rows of pinnules present on inner margins of basis of legs 1 to 4 and on unarmed inner margin of first exopodal segment of legs 2 and 3. Slender spinules present on unarmed outer margins of exopodal segments of legs 2 to 4. Other fine ornamentation as shown in figures. Intercoxal sclerites present in legs 1 to 4.

Fifth legs reduced, represented by 2 pairs of sparsely plumose setae originating on mid ventral surface of somite, near posterior margin (Fig. 6A-B). Sixth legs represented by unarmed opercula closing off genital apertures (Fig. 6A).

DESCRIPTION OF MALE *Mormonilla minor*

Body slender, cyclopiform (Fig. 7A-B); prosomal and urosomal segmentation as in *M.phasma*. Body length of figured specimen 0.83 mm; range 0.75 to 0.84 mm (based on 3 specimens). Two pairs somitic sensilla present near posterior margin of dorsal cephalic shield; single pair present dorsally on pedigerous somites 2 to 5 and on genital somite. Rostral region with pair of sensilla as in *M.phasma*. Caudal rami (Fig. 7C) elongate, about 14 times longer than wide; armed with 6 setae; seta I lacking, seta II located 25% of distance along ramus, setae III–VI positioned around distal margin, seta VII located dorsally on rear margin. Ramus ornamented with fine denticles medially.

Antennules and maxillipeds exactly as in *M.phasma*. Differences in other cephalosomatic appendages as follows: exopod of antenna (Fig. 10B) 8-segmented, with an additional distal fusion between ancestral segments IX and X. Setation formula 1,0,0,0,0,1,1,4. Mandible (Fig. 8A) with similarly reduced coxal gnathobase lacking any distal blades; segmentation and setation formula of rami as in *M.phasma* but with 2 setae on apex of exopod much smaller. Maxillule (Fig. 10C) with very reduced praecoxal arthrite; fused coxa and basis bearing only single seta; endopod with 3 distal setae and lateral setae on exopod smaller than in *M.phasma*. Maxilla (Fig. 10D) with setiform element at middle of medial margin rather than spinous process as in *M.phasma*.

Swimming legs 1 to 4 (Figs. 8C, 9A-D) with basic segmentation as in *M.phasma*. Coxa and basis partly fused in legs 2 to 4. Spine and setal formula as follows:

	Coxa	Basis	Exopod	Endopod
Leg 1	0–0	0–0	I–0;I–1;II,I,3	0–0;0–0;0,2,1
Leg 2	0–0	0–0	0–0;0–1;I,I,3	0–0;0–0;0,2,1
Leg 3	0–0	0–0	0–0;0–1;0,I,3	0–0;0–0;0,2,1
Leg 4	0–0	0–0	0–1;0–1;0,I,2	0–0;0–1;0,2,1

Outer margin spine on third exopodal segment of leg 2 (Fig. 9D) fused to segment basally. Ornamentation sparse; basis without inner rows of pinnules; pinnules present on inner margins of first exopodal segment of legs 2 and 3. Other fine ornamentation as shown in figures. Intercoxal sclerites present, unarmed. Fifth legs (Fig. 8B) represented by 4 setae but setae naked and relatively longer than in *M.phasma*. Sixth legs (Fig. 8B) unarmed, ornamented with 4 short rows of fine spinules.

REPRODUCTIVE BIOLOGY OF *Mormonilla*

Mormonilla females have paired ovaries and paired oviducts, both of which open via the single median genital aperture on the genital double somite. They produce a pair of small egg sacs, each containing 2 eggs arranged antero-posteriorly. Both sacs emerge from the common median aperture, presumably one from each oviduct. Males have a single testis located medially in the prosome about at the boundary between cephalosome and first pedigerous somite (stippled in Fig. 1A-B). The single vas deferens forms a loop in the second and third pedigerous somites, then passes into the urosome to open on the left side of the genital somite. The vas deferens is not highly differentiated into specialised regions. The extruded spermatophore (Fig. 10E) is ovoid, has a slender neck and, after being placed on the female during copulation, discharges directly into the copulatory pore located within the median genital aperture.

DISCUSSION

Mormonilla displays extreme sexual dimorphism. The dimorphism in urosome segmentation, with the male possessing separate genital and first abdominal somites, and in antennule structure, with the male having geniculate antennules, is typical of podoplean copepods. The use by the male of geniculate antennules to grasp the female during mating is a primitive attribute of calanoids and podoplean copepods, although it has been secondarily lost in the Poecilostomatoida and in some representatives of other orders.

The male antennules are described above as indistinctly 8-segmented and even these few segments are poorly differentiated. The best defined articulation is the geniculation that separates the slender distal segment from the rest of the limb. Since the presence of the geniculation between ancestral segments XX and XXI of the male antennule is an apomorphy of the Neocopepoda we believe that it is reasonable to assume that the well defined geniculation in *Mormonilla* is homologous with the neocopepodan geniculation. On the basis of this assumption the distal segment is treated as homologous with ancestral segments XXI to XXVIII. A compound segment formed by the fusion of these same ancestral segments is present in males of the order Monstrilloida. The precise location of aesthetascs on antennules provides reference points that have proved very useful in determining segmental homologies in copepods (Huys & Boxshall, 1991). The 3 aesthetascs on the part of the male antennule proximal to the geniculation were tentatively identified as those derived from segments VII, XI and XVI, by Huys & Boxshall (1991). The aesthetascs on these particular segments are very conservative in podoplean copepods. For example, the male of the misophrioid *Archimisophria discoveryi* Boxshall retains only 4 aesthetascs on the part of the antennule proximal to the geniculation, on segments III, VII, XI and XVI. The males of harpacticoids retain a maximum of 2 aesthetascs on the proximal part of the antennule, on segments XI and XVI. In the male of the primitive siphonostomatoid *Ecbathyrion prolixicauda* aesthetascs are retained on segments I to IV, VII, IX, XI, XIV, XVI and XVIII in the proximal part. Even in gymnoplean copepods, which typically retain aesthetascs on many segments, it is possible to find examples with few aesthetascs remaining in males, such as *Stephos lucayensis* Fosshagen which retains aesthetascs only on segments III, VII, XI, XVI and XX in the proximal part of the male antennule.

The conservative nature of the aesthetascs on segments VII, XI and XVI in a wide range of copepod taxa supports the interpretation of the aesthetasc-bearing segments as the same 3 segments in *Mormonilla* males. This is reinforced by careful examination of the relative lengths of setae on the antennulary segments. Primitively the antennules of the Neocopepoda show an ancestral pattern of long and short setae arranged on particular segments. The basic pattern is best retained in modern calanoids. In *Ridgewayia wilsonae* Fosshagen, for example, a long seta is present on segments V,

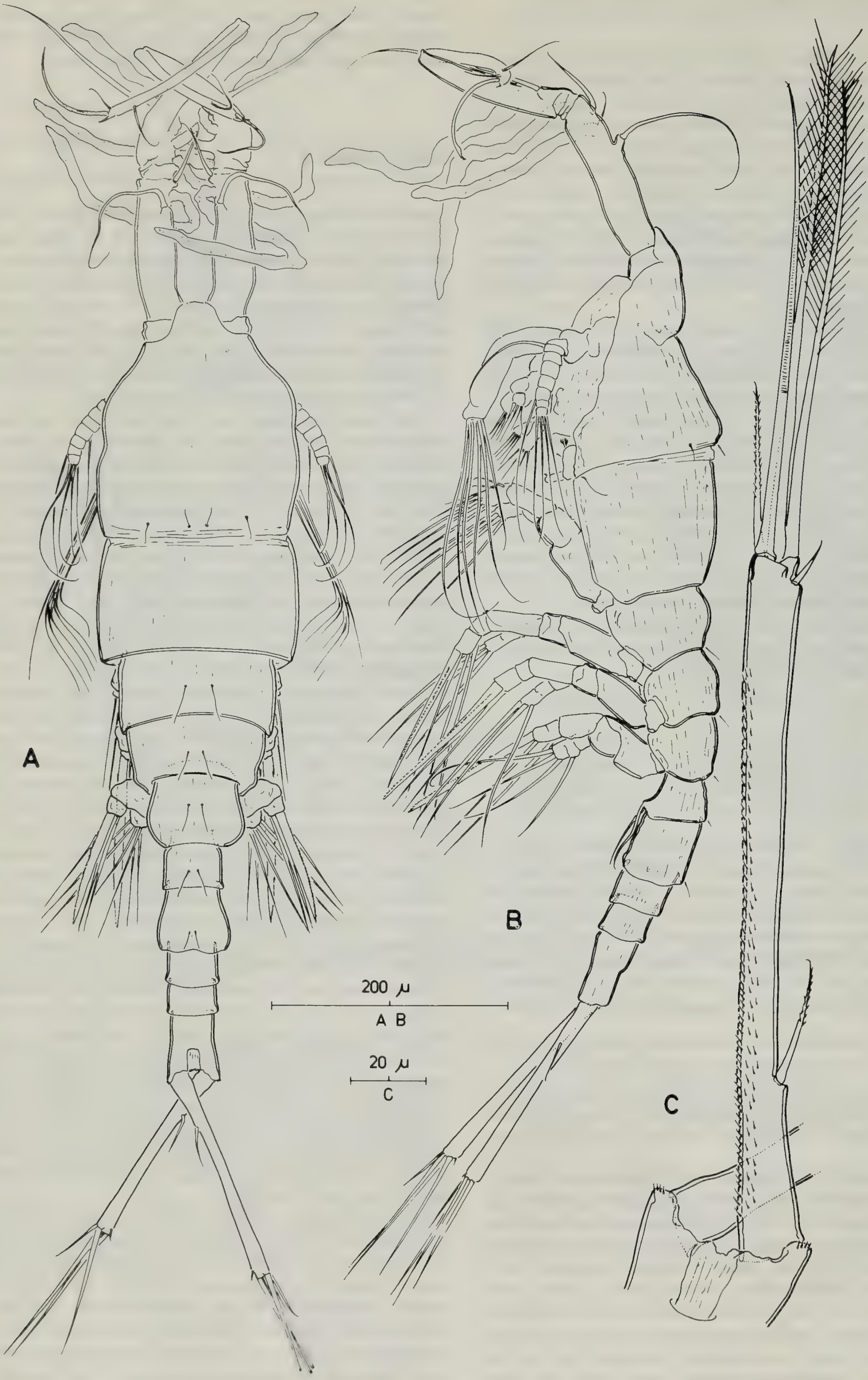
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Fig. 7 *Mormonilla minor* male. A, Entire, dorsal; B, Entire, lateral; C, Caudal ramus, dorsal.

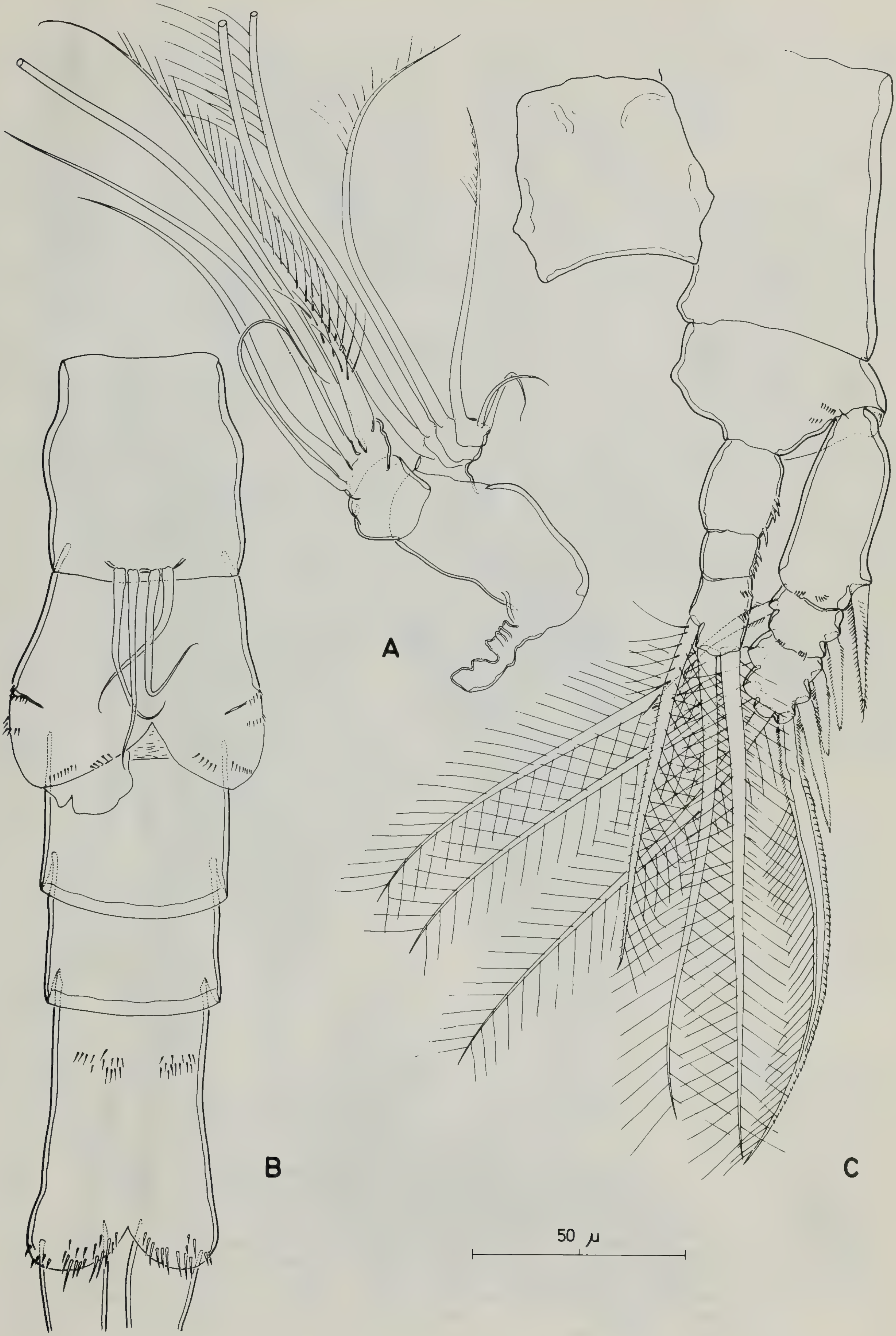

Fig. 8 *Mormonilla minor* male. A, Mandible, anterior; B, Urosome, ventral; C, First leg, anterior.

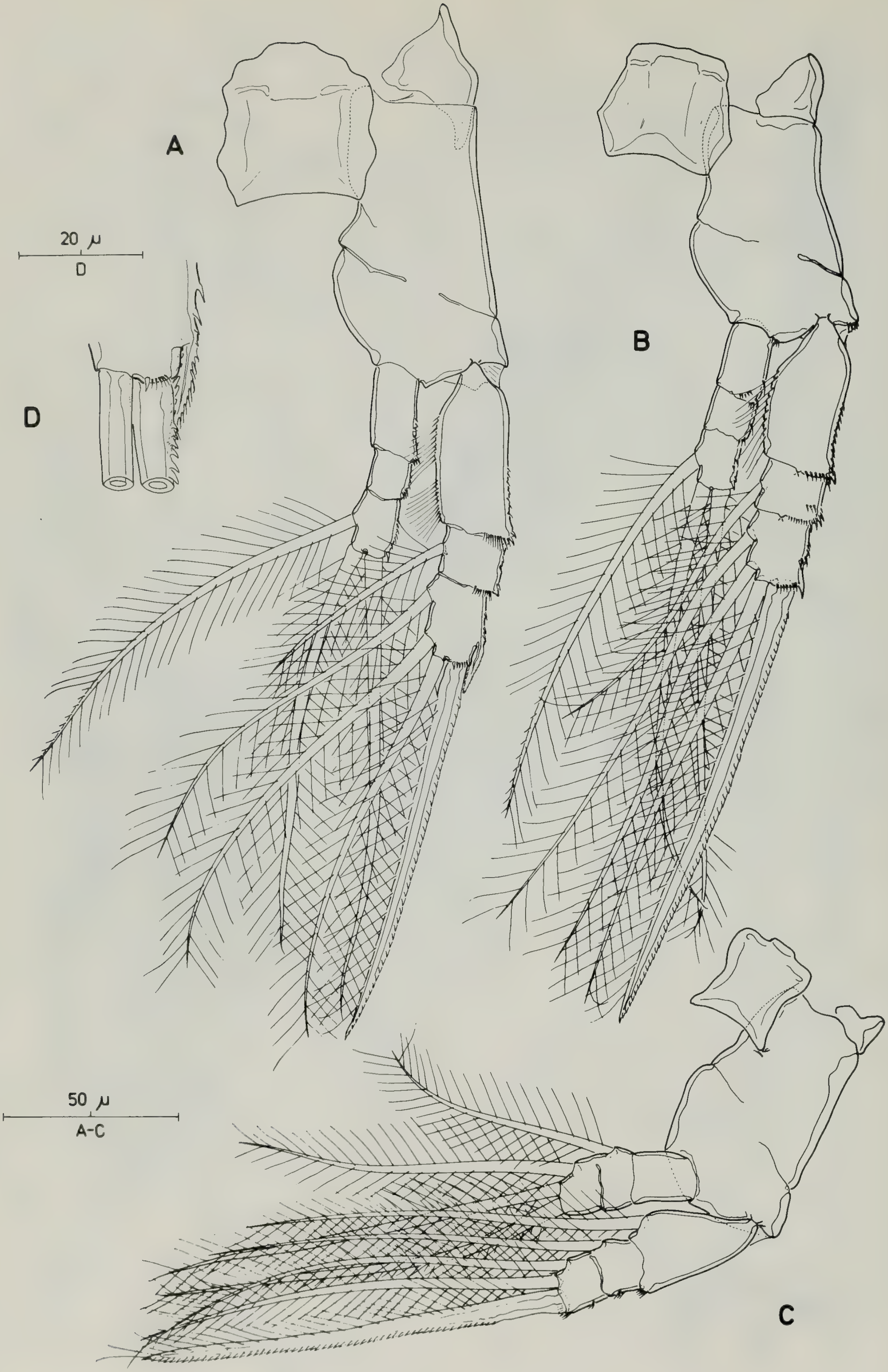

Fig. 9 *Mormonilla minor* male. A, Second leg, anterior; B, Third leg, anterior; C, Fourth leg, anterior; D, Detail of outer distal margin of exopod of second leg, anterior.

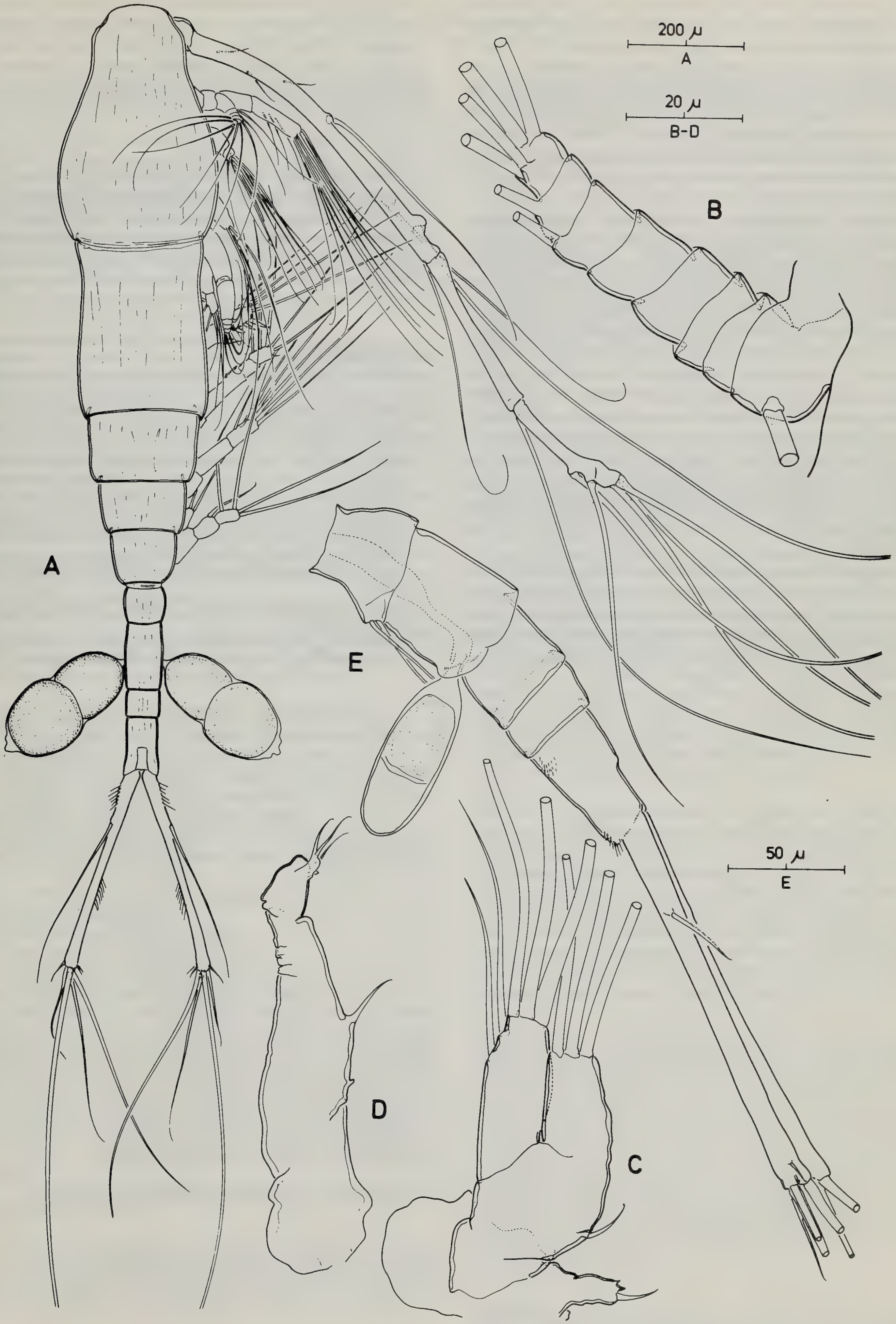

Fig. 10 *Mormonilla*. A, Ovigerous female *M.phasma*, dorsal. *M.minor* male. B, Antennary exopod, anterior; C, Maxillule, posterior; D, Maxilla, anterior; E, Urosome of male showing freshly extruded spermatophore, lateral.

IX, XI, XIV and XX, in the proximal part of the antennule (Huys & Boxshall, 1991: Fig. 2.2.2B). On the antennules of male *Mormonilla* there are 3 long setae present (Fig. 2A). If the identification of the aesthetasc-bearing segments is correct then the segments bearing long setae correspond well with ancestral segments V, IX and XIV. In our opinion this provides additional evidence in support of the interpretation of the segmental fusion pattern of the antennules of male *Mormonilla* as follows: I–VIII, IX, X, XI, XII, XIII, XIV–XX, XXI–XXVIII.

The sexual dimorphism in the other cephalosomatic appendages is very pronounced, especially in the more posterior limbs, i.e. the maxilla and maxilliped. The antenna of the male differs from that of the female primarily in the retention of separate first and second exopodal segments (these segments are fused in the female) and in the complete fusion of endopodal segments 2 and 3 (which are incompletely fused in the female). In addition a considerable number of setation elements present in the female are lost in the male. Differences in the mandible and maxillule are the gross reduction of the coxal gnathobase of the former and praecoxal arthrite of the latter. The palps of both appendages also show reductions in either segment numbers or setation. Both the maxilla and maxillipeds are reduced to tapering lobate structures bearing a few weak setae, except for a single well developed seta on the maxilliped.

All the postantennary mouthparts are very reduced in the male and the parts of the limbs most closely associated with processing food particles in the female are relatively more reduced than other parts. For example, the coxal gnathobase of the mandible is more reduced than the mandibular palp. Collectively these reductions can be interpreted as evidence that the adult male is a non-feeding stage. Functions performed by these limbs in the female that are not directly related to the particle-handling aspect of feeding, such as slow swimming movements, may still be carried out by them in the adult males.

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